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Are Age-Structured Models Appropriate for Catch-Effort Data?

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Ludwig, D., and C. J. Walters. 1985. Are age-structured models appropriate for catch-effort data? Can. J. Fish. Aquat. Sci. 42: 1066–1072.

Simulated data have been used to evaluate the performance of schemes for estimating optimum fishing effort using a simple stock-production model and R. B. Deriso's age-structured model. Even when the data are generated using Deriso's model, the simpler production model generally gives as good or better estimates for the optimal effort. The only exception to this result is when data are provided with unrealistically large contrasts in effort and catch per unit effort over time. The implication of these findings is that simple production models should often be used in stock assessments based on catch/effort data, even when more realistic and structurally correct models are available to the analyst; the best choice depends on how much contrast has occurred in the historical effort and catch per unit effort data, rather than on prior knowledge about which model structure is biologically more realistic.

Les auteurs ont utilisé des données simulées pour évaluer le rendement de plans d'estimation de l'effort de pêche optimum, à l'aide d'un simple modèle de production de stock et du modèle de R. B. Deriso structuré selon l'âge. En général, le simple modèle de production fournit des estimations aussi bonnes, voire meilleures de l'effort optimal même quand les données sont obtenues du modèle de Deriso, avec une seule exception : quand il y a beaucoup trop d'écart entre les données sur l'effort et les prises par unité d'effort en fonction du temps. Ces résultats indiquent que de simples modèles de production devraient souvent être utilisés pour les évaluations de stock basées sur les données de prises et d'effort, même quand des modèles plus réalistes et structurellement corrects sont disponibles; le meilleur choix dépend de l'écart qui s'est produit dans les données historiques sur l'effort et les prises par unité d'effort et non d'une connaissance antérieure du modèle le plus biologiquement réaliste.

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Simple surplus production models have been widely used in fisheries management, but they suffer from lack of biological realism. In recent years, as computers have become more powerful, more elaborate models and estimation schemes have become feasible (Deriso 1980). It seems obvious that greater biological realism will lead to better estimates for variables such as optimal exploitation rate or optimal effort. However, the more elaborate the model is, the greater are its requirements for information. It is possible for difficulties associated with parameter estimation to degrade the performance of age-structured models below that of simplistic stock-production models.

In this paper we show that a simple surplus production model derived from Ricker's model for stock and recruitment can perform as well as Deriso's (1980) age-structured model for stock biomass dynamics, even when the catch/effort data series is generated by Deriso's model in the first place. Here, performance is tested by means of simulations with artificially generated data series. Such tests are an indispensible supplement to tests on actual fisheries data, since a model and estimation scheme may produce plausible parameter values, which are nevertheless extremely inaccurate or misleading. We argue that all estimation schemes should be tested with simulated data where the parameter values are known in advance, since accuracy and consistency cannot in principle be determined from "real data" where the parameters are unknown.

A Ricker Model for Surplus Production

By pretending that fishing is concentrated in a short period each year with fishing mortality rate proportional to effort, and that biomass of the following year will be related by a dome shaped curve to the stock remaining after harvest, it is simple to devise the following surplus production model:

$$B_{t+1} = S_t \exp(\alpha - \beta S_t + U_t) \quad (1)$$

$$S_t = B_t - C_t \quad (2)$$

$$C_t = B_t(1 - \exp(-qE_t)) \quad (3)$$

where B_t denotes the population biomass in year t, S_t denotes the biomass remaining after harvest in year t, C_t denotes the harvest in year t, E_t denotes the observed effort in year t, U_t are independent normally distributed random variables, with mean 0 and variance σ^2, and α, β, and q are parameters to be estimated from catch and effort data.

A parameter estimation scheme for this model is detailed in Ludwig and Hilborn (1983). The basic procedure is to seek estimates of α, β, and q that minimize the sum of the squared residuals in $\ln(B_{t+1}/S_t)$ when equations (1)–(3) are fitted to catch and effort data. Here, we use a simpler formulation than theirs, since we neglect the effect of errors in estimating effective effort. This is done to simplify the presentation, and to save computer time when considering test data. However, such

observation errors should not be neglected when employing actual data. In the absence of observation errors, the estimation procedure involves the following iterative scheme: (i) assume a value for q and compute B_t and S_t using equations (2) and (3); (ii) estimate α and β from linear regression of $\ln(B_{t+1}/S_t)$ on S_t using B's and S's from step (i); (iii) repeat steps (i) and (ii) while varying q so as to find that value where the sum of the squared residuals is minimized. Various search procedures for function minimization may be used at this stage.

The following results are derived in Appendix A: after α, β, and q have been estimated, an optimum spawning stock S can be determined by choosing S to maximize discounted yield at equilibrium:

$$\delta S \exp(\alpha - \beta S + 1/2\sigma^2) - S = \text{maximum at } S = \hat{S} \tag{4}$$

where the discount factor $\delta = 0.9$. This corresponds to a 10% discount rate per year or per generation, depending upon the situation. Then the optimal effort is estimated by

$$\hat{E} = \frac{\alpha - \beta\hat{S} + \frac{1}{2}\sigma^2}{q}. \tag{5}$$

The Deriso Model

The model of Deriso (1980) considers two categories of biomass. If P_t denotes the biomass of prerecruitment juveniles and B_t denotes the biomass of catchable adults, prior to harvest in year t, then equation (8) of Deriso states that

$$P_{t+1} = (1 + \rho)\, lmP_t - \rho(lm)^2 P_{t-1} + R_{t+1} \tag{6}$$

$$R_{t+1} = (1 + \rho)S_t - \rho l^2 \frac{S_t}{B_t} S_{t-1} + (1 - m)P_{t+1}. \tag{7}$$

Here, ρ denotes the Brody growth coefficient (weight growth is assumed to be described by $W_{a+1} = W_k + \rho W_a$, where W_k is weight at recruitment and W_a is weight at age a). The fraction lost due to natural mortality is $1 - l$, and $1 - m$ denotes the fraction of individuals in P_t that become catchable in year t. Recruitment is assumed to depend only upon spawning biomass k years earlier:

$$R_{t+1} = S_{t+1-k} \exp(\alpha - \beta S_{t+1-k} + U_t). \tag{8}$$

This model assumes that random effects and density dependence are important only in the very early life stages. The concentration of these effects in the recruitment equation (8) greatly simplifies the analysis. We shall assume that catch and effort are related by (3), as before.

Although (1) and (8) are similar in appearance, their significance is quite different. This becomes apparent when α and β are estimated by linear regression. In the computations for the Deriso model, one must estimate P_{t+1} from (7), while using catch and effort data and equation (3) to estimate B and S for years $t - 1$, t, and $t + 1$. Then, R_{t+1} is estimated in terms of P_{t+1}, P_t, and P_{t-1}.

Thus, the calculation of R_{t+1} involves data from years $t + 1$, t, $t - 1$, $t - 2$, and $t - 3$. If S_{t+1-k} appears in that list, then 5 yr (generations) of catch and effort data are involved in the estimation of R_{t+1}; otherwise, 6 yr (generations) of data are involved. In contrast with the Deriso model, the regression for the Ricker model involves only 2 successive yr (generations) for each data point.

These complications make it awkward to compensate for observation errors when using the Deriso model. Nevertheless, a scheme analogous to the procedure in Ludwig and Walters (1981) and Ludwig and Hilborn (1983) has been devised and coded. It indicates that estimation performance deteriorates rapidly when observation errors are present. However, such a scheme is costly to run, so that extensive simulation trials are extremely expensive. Therefore, we have conducted our comparison on data without observation errors.

The estimation of parameters for the Deriso model is described in detail in Appendix B. The following is a summary of that description. In the absence of observation errors, parameter estimation for q, α, and β in the Deriso model proceeds as with the Ricker model, with one added step: (i) assume q and estimate R_t and S_t from equations (3) and (1); (ii) using the B_t and S_t estimates from step (i), solve equation (7) for time series of P_t estimates and then use these in equation (6) to solve for a time series of R_t estimates; (iii) regress the resulting estimates of $\ln(R/S_{t-k+1})$ versus S_{t-k+1} to get α and β; (iv) repeat steps (i)–(iii) while varying q so as to search for that value that maximizes the likelihood function. The negative of the log likelihood function is given by

$$-\ln L = \frac{n}{2}\frac{1}{n-2}\sum_{t=1}^{n} U_t^2 + \sum_{t=1}^{n} \ln W_t \tag{9}$$

where n is the number of regression points and W_t is the contribution of the current year's recruitment to the current year's catch. The second sum in (9) comes from the Jacobian of the transformation of the random variables $U_1, \ldots, U_n$ to the catches $C_1, \ldots, C_n$, which are the observations. Since this Jacobian involves q, it must be included in the likelihood function. If it is omitted, the performance of the Deriso scheme degrades very rapidly when the data have low contrast. Its importance was pointed out to us by J. Schnute (Pacific Biological Station, Nanaimo, B.C. V9R 5K6).

After the parameters in the Deriso model have been estimated, optimal $\hat{S}$ and $\hat{E}$ may be calculated, in analogy with (4) and (5). Details of the following calculations are given in Appendix C. It follows from (6), (7), and (8) that if E is held constant, then

$$S = \frac{1}{\beta}\Big[\alpha + \tfrac{1}{2}\sigma^2 - \ln(1 - (1 + \delta)lm + \delta l^2 m^2) + \ln(1 - m) - \ln(e^{qE} + \delta l^2 e^{-qE} - (1 + \delta)l)\Big]. \tag{10}$$

The discounted harvest at equilibrium is maximized if

$$\delta e^{qE} S - S = \text{maximum}. \tag{11}$$

In our calculations, a discount factor of 0.9 was chosen. The optimal effort $\hat{E}$ was determined from (11). Similar results were presented by Deriso (1980).

Simulation Trials

Some simulated catch and effort data are illustrated in Fig. 1. Initially, the stock was in a nearly unexploited state. Five years of low effort were followed by 10 yr of high effort, followed by a recovery period with low effort of 10 yr. Such sequences of efforts provide high contrast in both effort and catch per unit effort. The data were generated from the Deriso model by employing such a predetermined effort sequence, using parameter values that correspond to a long lived, slow growing species. The parameter values used were $k = 5$, $l = 0.9$, $m = 0.3$, $\rho = 0.2$, $\alpha = -0.5$, $\beta = 1$, and $q = 1$. Parameter σ^2 was set at 0.09, to give realistically large random variations in recruitment.

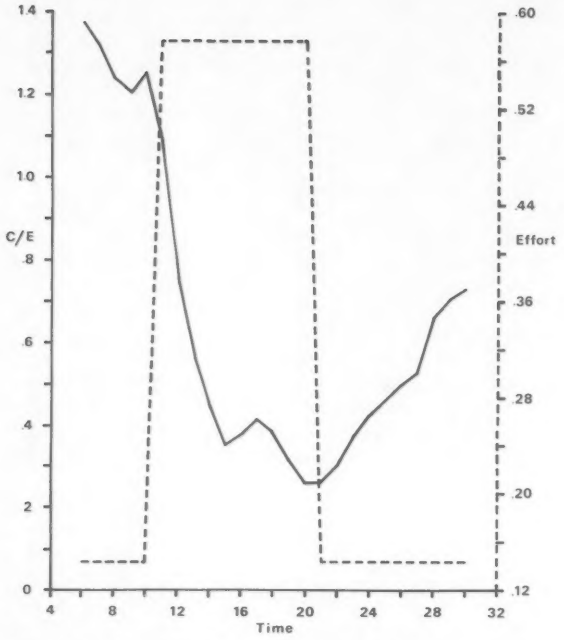

FIG. 1. Catch per unit effort (solid line) and effort (broken line) are plotted versus time for 25 yr of data. The data were generated by using the Deriso model with a set of pseudo-random normal deviates U_t, with $\sigma = 0.3$.

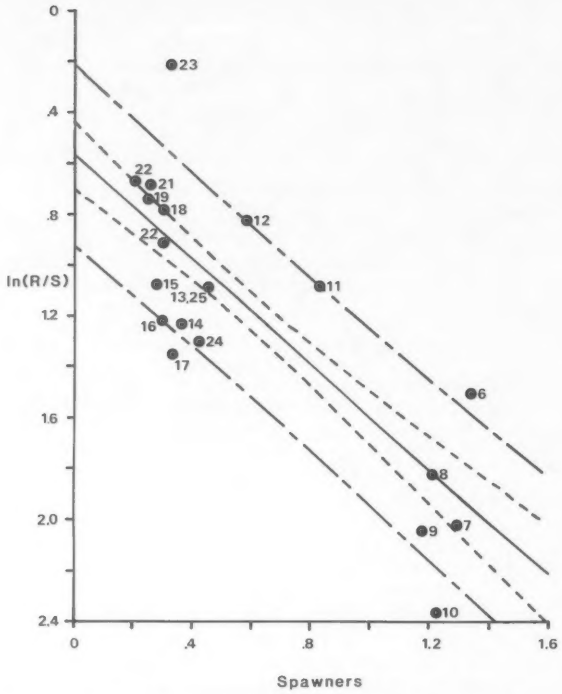

FIG. 2. Regression to determine stock-recruitment parameters using the Deriso model (negative logarithm of R/S versus the biomass of spawners). The solid curve is the least squares regression line. A 68% confidence band for the position of that line is given by the broken curves. The two outermost curves give 68% confidence limits for the position of the data points. The numbers next to the plotted points specify the year of spawning.

In parameter estimation trials, correct values for all but the last three parameters were assumed to be known a priori. That is, only q, α, and β were estimated from the data. With sufficiently informative data (i.e. with ratios of largest to smallest stock biomass and effort of at least 4), it is possible to estimate l in addition to α, β, and q. But attempts to estimate l and ρ together with the other three variables resulted in the likelihood function being maximized at impossible parameter values. This result is apparently at variance with Deriso (1980), who included seven parameters in his estimation procedure. However, he reported that the matrix of second partial derivatives was not positive definite at his estimated parameter values (p. 277), which implies that his optimization package did not find unique best estimates. We encountered similar difficulties when working with actual data from various stocks. We attribute this to a lack of contrast in the data, and to the effect of observation errors.

The Deriso and Ricker regressions to determine α and β given q (Fig. 2 and 3) are not directly comparable, due to differences in the underlying assumptions. For instance, note that the increases in catch per unit effort in years 15 and 16 are correctly attributed to high recruitment due to spawning in years 11 and 12, in the Deriso regression. But the Ricker regression attributes them to extraordinary recruitment in years 15 and 16. In spite of such differences, the two regressions are similar in one key respect: in both cases, information about the slope of the regression line comes mainly from the first few years (6–10) of data before the stock was heavily exploited, in combination with data from later years when the spawner biomass was low.

A series of simulation trials were performed to see how the performance of the estimation scheme would degrade as contrast in effort and catch per unit effort was reduced. Sequences of 25 yr of data and 50 yr of data were generated. Because when $k = 5$, the Deriso regression for 25 yr of data has only 20 points, we emphasize results from the 50-yr sequences. However, the results for 25-yr sequences were similar. Also, to make our theoretical point, ratios of high and low efforts as great as 8 were considered, although actual data from most fisheries would not be nearly so informative.

The results of the simulation trials are summarized in Table 1. The primary statistic is the average squared deviation of the estimated optimum effort from the actual optimum effort. Loss in long term harvest due to estimation errors is approximately proportional to that squared deviation, since the graph of the value function versus (constant) effort can be approximated by a parabola near the optimal effort. Thus, the average of the squared deviation can be interpreted as a percentage of the optimal harvest that may be expected. The performance of the Deriso model drops as contrast in effort is reduced. The drop in performance is also reflected in an increased number of failures in the estimation procedure. A "failure" was defined as any case where at least one parameter estimate was physically impossible, or where the estimated optimal effort differed by more than 50% from the actual optimum.

Note in Table 1 that the Ricker model scheme actually performed slightly better than the correct (Deriso) model when effort contrast (E ratio) was low. Though this advantage is perhaps not significant (statistically or for management), the accuracy of the estimates of optimal effort was slightly better

TABLE 1. Results of 150 simulation trials, using the Deriso and Ricker procedures to estimate parameters for 50 yr of data. The parameters in the simulation are intended to represent a slow growing fish. The first column gives the ratio of efforts prescribed, according to the scheme illustrated in Fig. 1. The maximum and minimum catch per unit efforts have a similar ratio. The performance of each method is best measured by the average of the squared deviation of the estimated optimal effort from the true optimal effort. This average is also converted into a percentage of the optimum yield that would be obtained by using the estimated optimal effort. The resulting percentage is displayed in the column headed "value." The bottom two lines are the result of 150 simulation trials for 50 yr of data, where efforts are given by a sequence of pseudo-random numbers. Each effort has the form $E = E^* \exp(U)$, where U is normally distributed with mean 0 and variance σ_u^2 and E^* is the optimal constant effort. The values of σ_u^2 are displayed in the first column under the heading "random." The parameters are chosen to imitate a slow growing fish.

	Deriso			Ricker		
E ratio	$\overline{(E-E^*)^2}$	Value (%)	Failures	$\overline{(E-E^*)^2}$	Value (%)	Failures
8	0.00038	99	0	0.00120	97	0
4	0.00094	98	0	0.00091	98	0
2	0.0027	92	9	0.00113	97	5
1.5	0.0038	91	27	0.00182	95	30
Random						
0.5	0.00263	94	0	0.00148	96	0
0.2	0.00293	93	15	0.00247	94	13

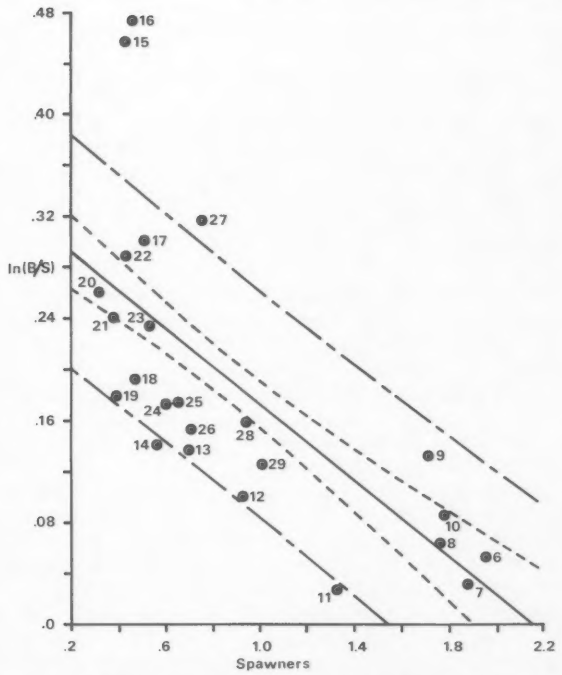

FIG. 3. Regression to determine stock-production parameters using the Ricker model (logarithm of B/S versus the biomass of spawners). The solid and broken curves have the same significance as in Fig. 2.

than when using Deriso's scheme. Since the Deriso model in fact had the correct structure, it outperformed the Ricker model when data with very large contrast were provided. But this advantage was lost when realistically low levels of effort contrast were tested.

One might suspect that this surprising result is due to the special form of the effort sequence used. To test this idea, pseudo-random sequences of efforts were generated, with varying degrees of expected contrast. figure 4 shows such a sequence of efforts. The results of 150 simulation runs are shown in Table 1. Again, the basic pattern is clear: the Ricker scheme performs about as well as the Deriso scheme at realistically low levels of contrast.

One might also suspect that our special choice of parameters was responsible for the good performance of the Ricker model. To test this idea, data were generated with Deriso's parameter estimates for haddock (*Melanogrammus aeglefinus*), a fast growing species for which a high exploitation rate is appropriate. The parameter values used were $k = 2$, $l = 0.51$, $m = 0.42$, $\rho = 0.85$, $\alpha = 1.1$, $\beta = 1$, and $q = 1$. The results (Table 2) are consistent with the preceding results; the Ricker scheme is almost as good as the correct Deriso model, except that more estimation failures occur at low effort contrast. We emphasize that the Deriso model also requires that parameters m, l, and ρ be specified or estimated. This requirement, and the greater computational complexity, raises grave questions about its practical utility.

Why Does the Ricker Model Perform So Well?

A clue to understanding the good performance of the Ricker model comes from comparison of Fig. 2 and 3. Although the two regressions are similar, the vertical scales on the two figures are very different. The difference in $\ln(B/S)$ is approximately 5 times as great in the Deriso regression as in the Ricker regression. For data that correspond to $k = 2$ (imitation haddock data) the corresponding factor is 2.

This disparity in variation carries through to parameter estimates: the maximum likelihood estimates will have standard errors that differ by corresponding factors. Our statistic $(\hat{E} - E^*)$ is roughly proportional to the variance of the estimated $\hat{E}$. Therefore, other things being equal, the Ricker estimates should produce an estimated $\hat{E}$ whose variance is lower by a factor of 25

TABLE 2. Results of 150 simulation trials for 25 yr of data. The parameters in the simulation are intended to imitate the dynamics of a faster growing fish than in Table 1.

	Deriso			Ricker		
E ratio	$\overline{(E-E^*)^2}$	Value (%)	Failures	$\overline{(E-E^*)^2}$	Value (%)	Failures
8	0.00228	99.9	0	0.00384	99.9	0
4	0.00238	99	0	0.00261	99	0
2	0.0084	97.5	2	0.0090	97.5	4
1.5	0.0191	95	10	0.0124	96.5	20
Random						
0.5	0.0136	96.5	1	0.0192	95	20
0.2	0.0268	93	29	0.0168	95.5	20

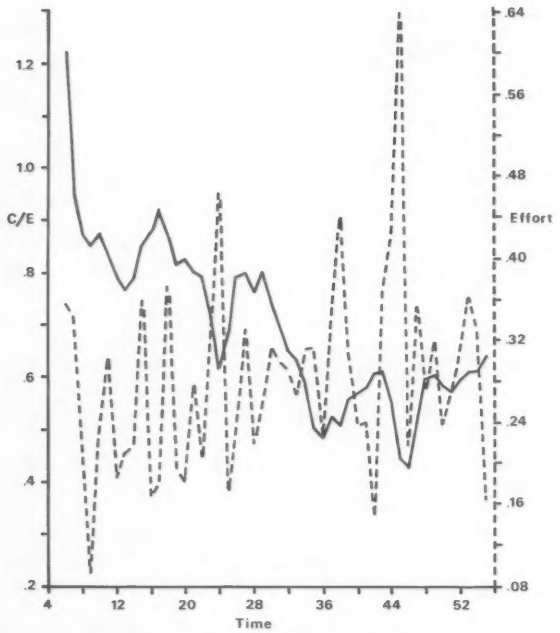

FIG. 4. Catch per unit effort (solid line) and effort (broken line) are plotted versus time for a pseudo-random sequence of efforts. The optimal effort E was multiplied by a log normally distributed pseudo-random number with mean 0 and standard deviation of 0.3.

when $k = 5$, and the Deriso ln (R/S) regression has 5 times the Ricker ln (B/S) standard error. Except when data are very informative, this advantage for the Ricker model cancels whatever advantage is provided by the superior structure of the Deriso regression.

To understand the difference in variation of ln B/S between the two models, we rewrite (7) in the approximate form

$$B = S[G + H \exp(\alpha - \beta(S - \bar{S}))]. \tag{12}$$

Here, G and H depend upon data from preceding years, and $\bar{S}$ denotes the mean spawning biomass. All of the density-independent growth and mortality is lumped into G, and H multiplies the density-dependent part, which is due to recruitment. For a long lived, slow growing species (for which age structure is presumably most important), H will be much smaller than G. Thus, we have approximately

$$\ln B/S \sim \ln G + \frac{H}{G} \exp(\alpha - \beta(S - \bar{S})). \tag{13}$$

The Ricker model consists in approximating (13) by

$$\ln B/S \sim \alpha^* - \beta^*(S - \bar{S}). \tag{14}$$

We have added asterisks to α and β in (14) to distinguish them from the corresponding quantities for the Deriso model. Comparing equations (13) and (14), we see that the amount of density dependence seen by the Ricker regression will be approximately H/G times the corresponding quantity for the Deriso regression.

A similar argument shows that this relationship also applies to variation in the estimated optimal effort, as computed by the two methods. Increasing the regression variance by a factor H/G results in correspondingly degraded estimates of optimal effort, unless the regression is provided with highly contrasting spawning stocks.

Conclusions

The phenomenon described above is not really surprising. It illustrates the general principle that the complexity of models and of decision procedures should be compatible with the amount of information available. Because of the large costs (direct and due to foregone harvest) of obtaining information about fish stocks, we suspect that management strategies in fisheries will always be developed in a twilight zone of inadequate information.

The implications are clear for models of population dynamics. The initial choice should be a minimal model that encompasses the basic variables that are measured (catch and effort), the decision variable (effort or exploitation rate), and a density-dependent effect, which determines desirable limits of stock abundance. Beyond that, each additional complication must be justified by the significance of its effect upon the basic variables, and by the adequacy of the information that is pertinent and available.

To obtain reasonable estimation performance with the Deriso model for data with moderate effort contrast, we had to assume correct values for ρ, l, m, and k. These parameters would ordinarily be estimated from age composition data. Therefore, even having more detailed data available to support some parameter estimates does not imply better performance of the more realistic surplus production model. Age-structured data do little to resolve uncertainties about q, since l (or its instantaneous rate equivalent M) and q are difficult to separate, as noted

graphically by Paloheimo (1980). However, such data may lead to improved estimation performance for α and β by providing more information about relative year class strengths.

Finally, we emphasize that the information that is important for management is primarily derived from variation in stock size. There is no way to estimate optimal biomass limits or exploitation rates without substantial contrast in effort and in catch per unit effort. This need for contrast is not unique to surplus production analysis; it is equally important for making valid inferences about detailed biological relationships such as density-dependent growth and juvenile survival. Therefore, we are not going to escape the statistical problems raised by surplus production analysis just by resorting to more careful biological investigations and detailed modelling.

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Appendix A: Optimal Catch and Effort Calculation for the Surplus Production Model

Here we assume that the stock can be maintained at a constant biomass after harvest, which will be denoted by S. The total expected discounted yield V is then given by

$$(A.1) \quad V = B - S + \sum_{t=1}^{\infty} \delta^t \left[\underset{U}{\mathcal{E}} [S \exp(\alpha - \beta S + U) - S] \right]$$

where δ is a yearly (or generational) discount factor and B is the initial biomass before harvest. Since U is assumed to be normally distributed with mean 0 and variance σ^2, the expectation is given by

$$(A.2) \quad \underset{U}{\mathcal{E}} [S \exp(\alpha - \beta S + U)] = S \exp(\alpha - \beta S + \tfrac{1}{2}\sigma^2).$$

Moreover, the sum on the right-hand side of (A.1) is a geometrical series. When these facts are employed, (A.1) becomes

$$(A.3) \quad V = B - S + \frac{\delta}{1-\delta} [S \exp(\alpha - \beta S + \tfrac{1}{2}\sigma^2) - S]$$

or

$$(A.4) \quad V = B + \frac{1}{1-\delta} [\delta S \exp(\alpha - \beta S + \tfrac{1}{2}\sigma^2) - S].$$

Therefore, V is maximized by maximizing (4), as claimed there.

That maximization may be performed efficiently as follows: (4) is maximized if $\hat{S}$ satisfies

$$(A.5) \quad (1 - \beta\hat{S}) \exp[\ln \delta + \alpha + \tfrac{1}{2}\sigma^2 - \beta\hat{S}] = 1.$$

If we define

$$(A.6) \quad A = \ln \delta + \alpha + \tfrac{1}{2}\sigma^2 - 1$$

$$(A.7) \quad T = 1 - \beta\hat{S}$$

then (A.5) may be rewritten as

$$(A.8) \quad T \exp(A + T) = 1.$$

The root T of this equation may be found by the following iteration scheme: let $T_0 = 0$, and

$$(A.9) \quad T_{n+1} = (1 + T_n)/(1 + \exp(A + T_n)).$$

The iterations converge rapidly to a root <1 if $A > -1$.

Once the root is found, we may solve (A.7) to obtain

$$(A.10) \quad \hat{S} = \frac{1 - T}{\beta}.$$

In order to calculate the corresponding effort, we note from (3) that the stock remaining after harvest is

$$(A.11) \quad S = B \exp(-qE).$$

Thus, assuming the expected increase in biomass, the appropriate effort is chosen so that

$$(A.12) \quad \alpha - \beta\hat{S} + \tfrac{1}{2}\sigma^2 - qE = 0.$$

i.e. so that the expected stock after harvest is $\hat{S}$. Thus, equation (5) follows from (A.12).

Appendix B: Likelihood Function for the Deriso Model

There is subtlety in the derivation of the likelihood function for the Deriso model, which requires an extended explanation. The likelihood function is derived from a density function on the space of possible observations, which expresses the probability density of such observations, given a particular set of parameters $\vec{p}$. In the case of the Deriso model, $\vec{p}$ will include q and any of the parameters ρ, l, m, and k that one attempts to estimate. The parameters α and β appear linearly at a crucial stage, and therefore they are treated separately. The efforts E_t are not regarded as random variables, but instead as "fixed inputs."

In the Deriso model (3), (6)–(8), the catches are determined in terms of the normally distributed random variables U_t; for the moment we write the corresponding density as $f(\vec{U}, \vec{p})\, d\vec{U}$, where $f(\vec{U}, \vec{p})$ is a product of one-dimensional Gaussian densities. It is important to recognize that $f(\vec{U}, \vec{p})$ is not the likelihood function, since the likelihood L is derived from a density on the space of possible catches. The connection between f and L is made by equating the corresponding elements:

$$(B.1) \quad L(\vec{C}, \vec{p})\, d\vec{C} = f(\vec{U}, \vec{p})\, d\vec{U}.$$

This connection implies that

$$(B.2) \quad L(\vec{C}, \vec{p}) = f(\vec{U}, \vec{p}) \frac{\partial(\vec{C})}{\partial(U)}$$

where $\partial(\vec{C})/\partial(\vec{U})$ is the Jacobian of the transformation from the random variables U to the observed C. For simple models such as the surplus production model, this Jacobian is present, but it does not depend upon the parameter to be estimated. Therefore it may safely be ignored. However, in the case of the Deriso model, the Jacobian depends strongly upon the parameter q, as will be seen below.

In order to calculate $\partial(\vec{C})/\partial(\vec{U})$, we first express (6) and (7) in terms of the observed catches and efforts. It follows from (2) and (3) that

$$(B.3) \quad S_t = C_t \frac{e^{-qE_t}}{1 - e^{-qE_t}}$$

and

$$B_t = \frac{C_t}{1 - e^{-qE_t}}. \quad \text{(B.4)}$$

Now (7) may be written in the form

$$\frac{C_{t+1}}{1 - e^{-qE_{t+1}}} = (1 - m)P_{t+1} + \ldots \quad \text{(B.5)}$$

where the dots denote terms that depend upon data from years (or generations) before $t + 1$. A similar treatment of (6) and a substitution produces

$$C_{t+1} = (1 - e^{-qE_{t+1}})(1 - m)(R_{t+1} + \ldots). \quad \text{(B.6)}$$

If (8) is employed in B.6, we finally see how U_t influences C_{t+1}. Earlier variables U_{t-1}, etc., also influence C_{t+1}, but no future variables such as U_{t+1} can have an effect. We conclude that the Jacobian $\partial(\vec{C})/\partial(\vec{U})$ is the determinant of a triangular matrix, and hence it is a product of diagonal elements. In fact, from (8) we have

$$\frac{\partial R_{t+1}}{\partial(U_t)} = R_{t+1}. \quad \text{(B.7)}$$

Therefore

$$\frac{\partial(\vec{C})}{\partial(\vec{U})} = (1 - m)^n \prod_t (1 - e^{-qE_{t+1}})R_{t+1}. \quad \text{(B.8)}$$

The preceding result may be inserted into (B.2) in order to compute the likelihood function. Since U_t are assumed to be normally distributed with variance σ^2, the log likelihood is given by

$$\ln L(C, p) = \frac{-1}{2\sigma^2} \sum_t U_t^2 - n \ln \sigma - n \ln (1 - m) - \sum_t \ln [(1 - e^{-qE_{t+1}})R_{t+1}]. \quad \text{(B.9)}$$

In the formulation (B.9), the parameter vector p includes α, β, and σ, as well as q, etc. The computation of parameter estimates becomes much more manageable if we divide it into two stages. In the first stage, q, etc., are fixed and α and β are estimated by an ordinary regression, i.e. by minimizing

$$\sum_t U_t^2.$$

Then σ is estimated by

$$\hat{\sigma}^2 = \frac{1}{n - 2} \sum \hat{U}_t^2 \quad \text{(B.10)}$$

where $\hat{U}_t$ is the residual when α and β are replaced by their least squares estimates $\hat{\alpha}$ and $\hat{\beta}$.

In the second stage, q and any additional free parameters are estimated by minimizing

$$-\ln L = n \ln \hat{\sigma} + \sum_t \ln [(1 - e^{-qE_{t+1}})R_{t+1}]. \quad \text{(B.11)}$$

This is the expression that appears in (9).

Appendix C: Optimal Catch and Effort Calculation for the Deriso Model

The calculation of optimal effort proceeds in analogy with Appendix A. The derivation (A.1)–(A.3) carries over, if the expression in square brackets is interpreted as a catch. Thus, (A.3) may be written as

$$\text{maximize} \left[-S + \frac{\delta}{1 - \delta} C \right] \quad \text{(C.1)}$$

as a function of the (constant) effort. From (2) and (3) it follows that

$$C = S(e^{qE} - 1). \quad \text{(C.2)}$$

If (C.2) is substituted into (C.1), the result is (11).

It still remains to calculate S as a function of E, assuming equilibrium conditions. This calculation involves (6)–(8). Assuming constant conditions and averaging as in (A.2), (6) becomes

$$P[1 - (1 + \rho)lm + \rho l^2 m^2] = S \exp [\alpha + \tfrac{1}{2}\sigma^2 - \beta S]. \quad \text{(C.3)}$$

If (C.3) is substituted into (7), the result is

$$\frac{[1 - (1 + \rho)lm + \rho l^2 m^2]}{1 - m} [e^{qE} - (1 + \rho)l + \rho l^2 e^{-qE}] = \exp [\alpha + \tfrac{1}{2}\sigma^2 - \beta S]. \quad \text{(C.4)}$$

If (C.4) is solved for S, the result is (10).

Yolk Absorption, Yolk Sac Constrictions, Mortality, and Growth During First Feeding of Atlantic Salmon (*Salmo salar*) Incubated on Astro-turf

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Hansen, T. J., and D. Møller. 1985. Yolk absorption, yolk sac constrictions, mortality, and growth during first feeding of Atlantic salmon (*Salmo salar*) incubated on astro-turf. Can. J. Fish. Aquat. Sci. 42: 1073–1078.

Groups of pooled Atlantic salmon (*Salmo salar*) eggs were incubated in a "California" incubation system with and without astro-turf, an artificial substrate, and later transferred to separate feeding units. Alevins reared in astro-turf absorbed their yolk sac faster and more efficiently than alevins reared on a flat screen. Alevins reared on the flat screen developed yolk sac constrictions probably due to the backward and lateral force created by the high swimming activity. No such malformations were found on the yolk sacs of the astro-turf reared alevins. The fry hatched without astro-turf grew faster than the fry hatched with astro-turf during the initial feeding period, but later this was reversed. Mortality of alevins and fry hatched with astro-turf was lower during incubation and during first feeding.

Des œufs de saumon atlantique (*Salmo salar*) ont été incubés en groupes dans des incubateurs californiens tapissés ou non de substrat artificial, puis transférés à des unités d'alimentation séparées. Les alevins élevés sur du substrat artificiel ont absorbé leur vésicule vitelline plus vite et plus efficacement que ceux qui étaient gardés sur un grillage plat. Ces derniers ont présenté des étranglements de la vésicule vitelline, probablement à cause de la force latérale et rétrograde créée par l'activité natatoire élevée. De telles malformations n'apparaissaient pas sur la vésicule des alevins élevés sur le substrat artificiel. Chez les poissons élevés sans substrat, la croissance était plus rapide au cours de la période d'alimentation initiale que chez ceux qui étaient gardés sur un substrat; cependant, cette tendance s'est inversée plus tard. Chez les alevins vésiculés et les alevins nageants élevés sur un substrat artificiel, la mortalité était moins élevée pendant l'incubation et la période d'alimentation initiale.

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In the Norwegian fish farming industry, traditional "California" (Edwards 1978) incubation systems are used almost exclusively. These systems improve survival from the green egg stage to the age at first feeding over natural production. However, blue sac and white spot disease and yolk sac constrictions, abnormalities that probably all are attributable to the hatchery environment, are very common and occasionally cause heavy losses. Moreover, the fry from these systems have been shown by several authors (e.g. Bams 1967; Mead and Woodall 1968) to have lower viability than naturally produced fry.

The practice of incubating salmonids in gravel or artificial substrates for enhancement purposes is well known (see Bams and Simpson 1977). Several authors (Marr 1965; Bailey and Taylor 1974; Leon 1975) have reported reduced size of fry incubated in flat screened hatching trays compared with these substrate incubators. Moreover, Bams (1972, 1974) has shown that fry from gravel incubators are very similar to naturally produced fry in characteristics such as yolk conversion efficiency (YCE), size at emergence, growth rate, and survival to the adult stage. They are also superior to Japanese-style hatchery (JSH) fry in YCE, size and stage at emergence, and timing of emergence (Bams 1982). However, surprisingly, JSH fry rated superior in terms of final size and growth rate during 8 wk following emergence (Bams 1983).

The purpose of this experiment was to investigate what advantages would be gained in a commercial hatchery by introducing astro-turf as an artificial substrate. Special attention was given to the phenomenon of yolk sac constrictions on which both descriptive and causative information is lacking.

Materials and Methods

Freshly fertilized Atlantic salmon (*Salmo salar*) eggs were obtained from a commercial fish farm (Torris laks, Halsa) and were held at a mean temperature of 6.5°C. When the eyed egg stage was reached, eggs from a number of females were pooled and six groups of 6700 eggs (1.2 L) were placed in separate hatching trays. An EWOS traditional Californian hatching

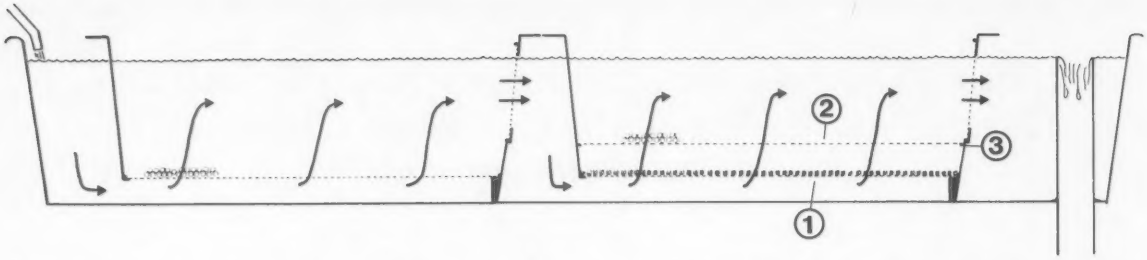

FIG. 1. Side view of a traditional and a modified hatching tray. Modifications: 1, astro-turf; 2, perforated plastic screen; 3, plastic strips. Arrows indicate the water direction.

system was used, but three trays were modified as outlined in Fig. 1. Backless polyethylene astro-turf was sewn to the perforated aluminum bottom and a plastic screen with 3 × 20 mm perforations was laid loosely on plastic strips mounted just below the water level. The rest of the trays were used in the traditional manner without modifications.

In the modified trays the eggs were placed on the perforated plastic screens. After hatching, the alevins swam through the holes and into the astro-turf whereas the dead eggs remained on the screen where they could not foul the substrate. After hatching, the perforated plastic screens were removed from the trays.

Water input to the array was 10 L/min and the temperature varied between 7.0 and 5.6°C with a mean of 6.3°C.

At commencement of first feeding, 5000 fry from each group were transferred to separate feeding units (1 m^2 in area). Another 500 fry were maintained in their original hatching tray to follow the development throughout the yolk sac period, uninfluenced by feeding. The remaining 1000–1250 fry from each tray were excluded from the experiment.

The feeding groups were fed commercial dry feed pellets (EWOS ST40 No. 1, particle size 0.25–0.8 mm) (Table 1) in surplus with automatic feeders. Feed was offered six times an hour and 24 h a day. After 19 d of feeding, about 1800 fish in one of the groups died because of an accidental stoppage in the water supply. Consequently, all the groups were reduced to 3200 fry and kept at this density throughout feeding.

When the first feeding began (41 d after hatching) the water input was 8 L/min to each feeding unit. The mean temperature was 12.4°C, but during two periods of 3 d the temperature fell below 10°C.

Samples of 10–40 larvae from each hatching tray were collected and preserved in 5% formalin every 3 d from 50% hatching until the fish were transferred to the feeding units. The modified trays were not sampled at day 0 when the plastic screens still covered the larvae. The fish in the unfed groups were sampled four times between days 41 and 76. Four times during first feeding the fry were crowded in their feeding units, and 60–100 fry were collected for wet weight measures.

Samples were kept in the preservative for 6 wk or more after which alevin total length was measured to the nearest millimetre downwards ($d = \pm 0.5$ mm). Yolk sac length was measured using a binocular microscope with a measuring ocular. The alevins were dried to constant weight (at least 48 h at 60°C). Following this, alevins and yolk sacs were weighed separately on an electronic microbalance ($d = \pm 0.1$ mg). Individual body weight (total weight minus yolk sac) was then calculated. The YCE for the different periods was calculated based on body weight and yolk weight, using the dry weight method of Blaxter (1969). Yolk sac constrictions were cut off and weighed en masse for each sample group.

TABLE 1. Composition of the EWOS ST40 commercial dry feed.

Component	Weight (%)
Fishmeal (Norsemink)	55.0
Steamed carbohydrates	11.5
Capelin oil	12.0
Yeasts	5.0
Binder	2.5
Bloodmeal	10.0
Minerals	2.0
Vitamins	2.0

Individual live fry from the feeding groups were blotted to remove excess water and were immediately weighed to the nearest milligram on the electronic microbalance to obtain total wet weight.

The data were statistically analysed by BMDP statistical software (Dixon 1981). A confidence level of 5% was adopted in all tests. Differences in body and yolk sac dry weights, in the relation between length and dry weight, in yolk sac lengths, and in the first feeding wet weights were compared using an F-test for equality of variances and later a Student t-test for separate or pooled variances. The same tests were used for comparisons of mortality during different periods of the experiment. Percent data were transformed to inverse sine values to normalise their distribution.

Results

Alevins reared in astro-turf (ATR) were significantly heavier ($p < 0.001$) 9 d after hatching than those reared on a flat screen (FSR) (Fig. 2). This difference increased to a maximum of 7.2 mg at day 46. At the point of greatest body weight for the ATR alevins (day 53) the difference was 6.8 mg, whereas at the point of greatest FSR alevins body weight (day 67) the difference was 5.3 mg. Moreover, from mean length greater than or equal to 19 mm, the ATR alevins were significantly heavier than FSR alevins of the same length (Fig. 3).

The yolk absorption rate was nearly constant from hatching throughout the alevin stage in both systems. However, the ATR alevins absorbed their yolk sac faster than the FSR alevins, having a significantly lower ($p = 0.011$) mean yolk sac weight at day 21. Except for day 24 this difference remained significant

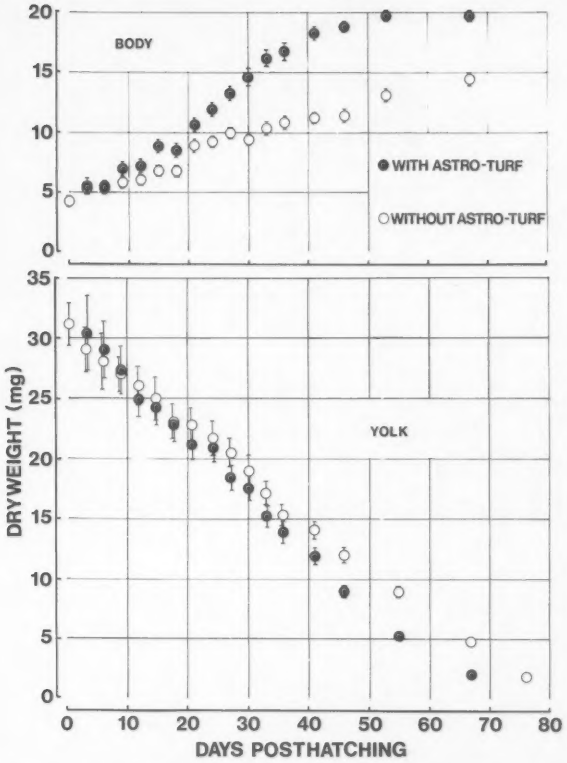

FIG. 2. Changes in dry weight over time of body (upper panel) and yolk (lower panel) in the two incubation systems. Vertical lines indicate 95% confidence limits.

throughout the experiment. On day 41, when most fish were transferred to the feeding units, the difference was 2.3 mg.

The YCE increased not only from the first to the second period in both systems, but also from the second to the third in the trays with astro-turf (Table 2). The corresponding drop in YCE for the FSR alevins resulted in the greatest difference observed betwen the systems. The first drop in YCE of the ATR alevins occurred from the third to the fourth period. A simultaneous increase in the YCE of the FSR alevins gave these the highest YCE during the last two periods.

Apart from three cases observed on day 15 and one each on days 27 and 33, no constrictions were found on the yolk sacs of the ATR alevins. However, in the FSR alevins the first constricted yolk sacs were found on day 6, and on day 33 all alevins had this malformation. The amount of constricted yolk per alevin peaked on day 21 with 3.1 mg (Fig. 4). This amounted to 13.6% of the total yolk mass on this day. The yolk behind the constrictions was, however, absorbed and no yolk was seen to be pinched off.

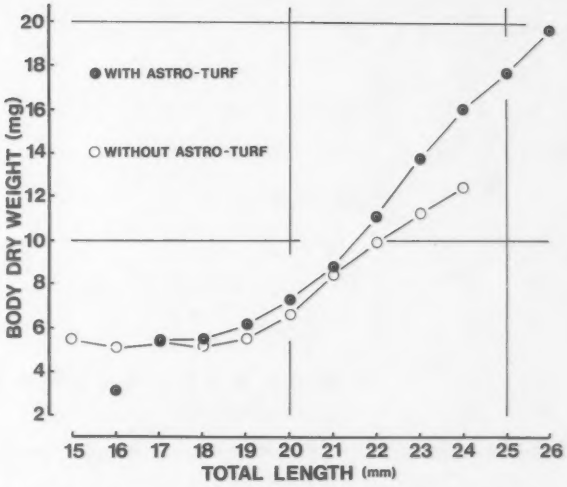

FIG. 3. Relationship between total length and body dry weight of fry from two incubation systems.

Mean yolk sac length increased rapidly from hatching until day 6 in both systems (Fig. 5). The increase was however greater in the FSR alevins than in the ATR alevins, giving a significant difference ($p = 0.035$) on day 6. Between day 6 and day 21 the yolk sac length remained rather constant in both systems but later fell rapidly while the yolk sac was being absorbed. Except for days 18 and 27 the difference remained significant.

The FSR fry grew faster than the ATR fry in the first period of feeding (Fig. 6). However, from feeding day 18 until the experiment was terminated at day 46 the ATR fry grew faster. The difference in mean wet weights of the fry from the two incubation systems was significant throughout the feeding period.

The ATR fish had significantly lower mortality than the FSR fish through all incubational periods and the first 18 d of feeding (Table 3). The total mortality during initial feeding (45 d) and during the whole experimental period (86 d) was also significantly higher in the FSR fish.

TABLE 2. Calculated YCE values (%) for different periods during the yolk absorption.

Rearing substrate	Period (d) 1st (3–15)	2nd (15–27)	3rd (27–41)	4th (41–53)	5th (53–76)	3–41[a]	3–53[b]	3–67[c]
Astro-turf	55.7	72.3	78.6	24.5	—[d]	68.0	57.1	50.1
Flat screen	38.1	68.8	21.2	35.0	26.0	40.2	38.9	37.4

[a]On day 41 the fry were transferred to feeding tanks.
[b]Day 53 is time of the greatest body weight of alevins reared on astro-turf.
[c]Day 67 is time of the greatest body weight of alevins reared on flat screen.
[d]Yolk conversion efficiency was not calculated due to negative body growth rate.

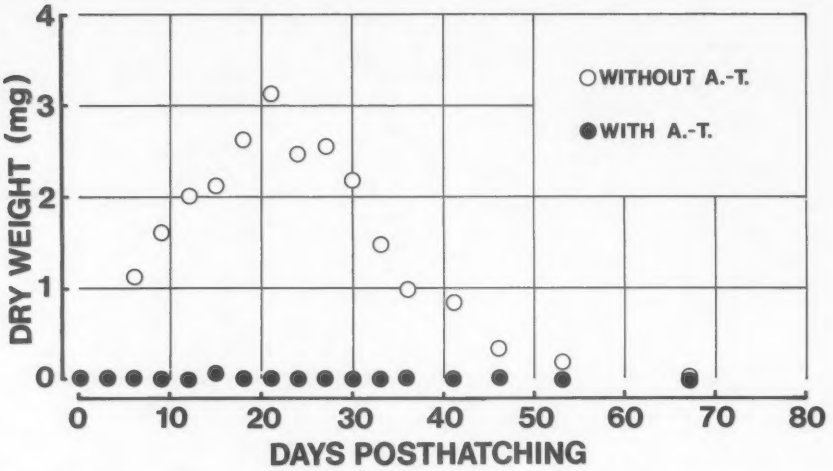

FIG. 4. Dry weight of yolk sac constrictions over time of alevins from the two incubation systems.

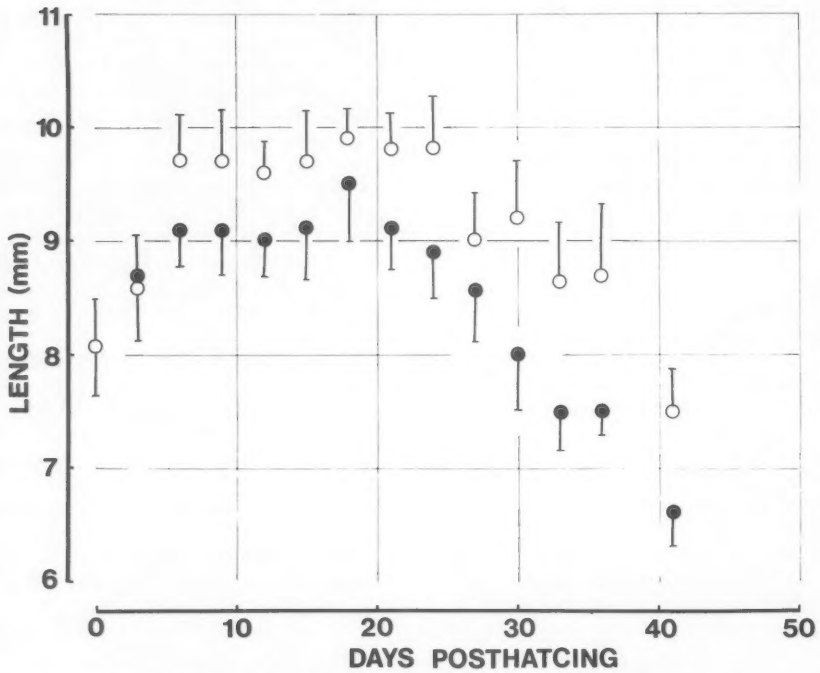

FIG. 5. Yolk sac length over time of fish in the two incubation systems.

Discussion

The difference in growth and hence final weight of the alevins in the two systems is explained by Marr (1963) and Bams (1969). They observed that falling over of alevins rearing on a flat surface was compensated by swimming activity which stabilised the alevins in the vertical plane (righting response), a phenomenon that also was observed in our experiment. Compared with alevins reared on a rugose substrate, these alevins consequently converted less yolk to body tissue. However, in our experiment a difference in absorption rate also contributed to the weight difference because the ATR alevins absorbed relatively more of their yolk during the period of high YCE.

We found the yolk absorption rate to be nearly constant from hatching and throughout the alevin stage, corresponding with results on sockeye salmon (*Oncorhynchus nerka*) (Brannon 1965). The higher absorption rate of the ATR alevins supports the findings of Leon (1975) who used plastic saddles as an incubation substrate. He proposed that this might be the result of oxygen depletion in the microenvironment of the FSR alevins.

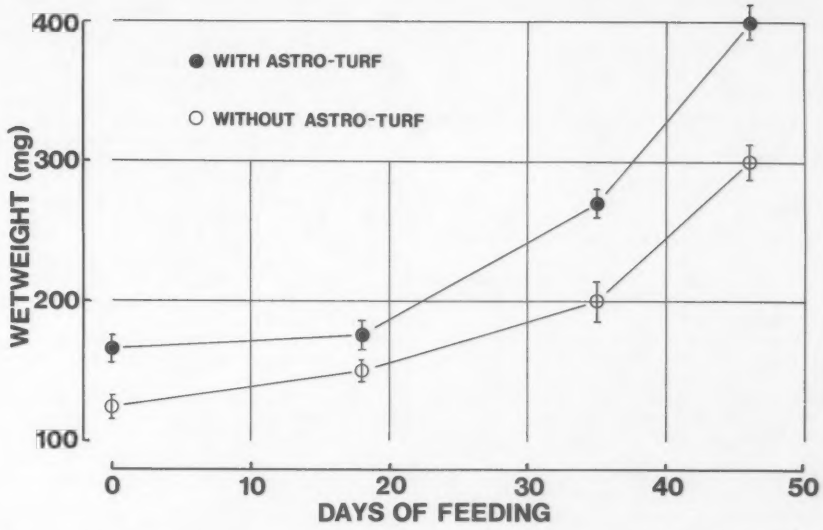

FIG. 6. Total wet weight over time during first feeding of fry from the two incubation systems. Vertical lines indicate 95% confidence limits.

TABLE 3. Mortality (%) during different periods of the experiment.

Period (d)	Treatment: Astro-turf	Treatment: Flat screen	Probability value (*t*-test)
Incubation			
0–9	0.26	0.69	0.006
9–18	0.03	0.79	0.014
18–41	0.44	2.86	0.032
0–41	0.73	4.34	0.005
Initial feeding			
0–18	0.70	1.57	0.014
18–33	1.00	1.43	0.187
33–45	1.92	3.33	0.131
0–45	3.62	6.33	0.082
Total	4.34	10.67	0.022

Hamor and Garside (1977) stated that low oxygen tension retarded yolk sac absorption in Atlantic salmon. It is, however, very unlikely that oxygen reached limiting concentrations given the rather high water input in our incubation systems. The high activity stress of the FSR alevins might, however, reduce the yolk absorption rate. Other stressors such as high temperatures (Hayes and Pelluet 1945), low oxygen saturation (Hamor and Garside 1977; Brannon 1965), suboptimal salinity (Lasker and Theilacker 1962), high concentrations of ammonia (Fedorov and Smirnova 1978), and sublethal concentrations of herbicides (Woodward 1976) are all known to reduce yolk absorption in fish larvae.

The increase in YCE in the first period after hatching is in accord with Gray's (1928) data on brown trout (*Salmo trutta*), but remains unexplained.

Flat-bottomed incubation trays are known to induce yolk sac constrictions in different *Oncorhynchus* species and hybrids (Emadi 1973) and in Atlantic salmon (Leon 1975; Gunnes 1979). D. Poon (pers. comm. cited in Emadi 1973) attributed this malformation to mechanical injury caused by continual rubbing on the flat surface. We do not concur with this explanation because such injury to the yolk sac causes water to intrude through the sore, coagulating the yolk and forming a white spot, and a white spot was not observed in this experiment. Yolk sac constriction appears associated with high swimming activity of alevins which creates a backward and lateral force on the yolk sac, causing it to elongate. As the sac gets slimmer and longer the swimming activity probably makes the posterior part of it move sideways and a constriction is formed.

If such a relationship holds, one would expect the problem to be aggravated by factors that increase the activity of the alevins. High temperatures have been shown to induce yolk sac constrictions (Emadi 1973; Dumas 1966) and so have high water velocities (Emadi 1973; Jochimsen and Bedell 1968). However, various substrates such as gravel (Emadi 1973), plastic saddles (Leon 1975), and astro-turf (this experiment) are known to resolve this problem, probably by lowering the activity of the alevins.

In the first feeding period the fry had low feeding activity and this could explain the low growth rate. Palmer et al. (1951) found for *O. nerka* and *O. tschawytscha* that feeding had little enhancing effect on the growth rate until the yolk was completely absorbed. As a consequence, fry with large yolk reserves, high YCE, or both could be favoured in the first period, as seen in the difference in growth rate between the two treatments in this experiment. This does not, however, agree with the results of Bams (1983) who demonstrated a steady growth rate only when the fry were fed early.

Hurley and Brannon (1969) did observe that fry of *O. nerka* with high yolk reserves had high mortality during initial feeding. This agrees with some of the differences in mortality that were found between our two treatments. However, on other salmonid species, and among them the Atlantic salmon (Atkins 1906), no connection between the timing of food introduction and mortality has been found. Wallace and Aasjord (1984) found that supraoptimal temperatures increased initial feeding

mortality in Arctic char (*Salvelinus alpinus*) and suggested that the high energy consumption at these temeratures prevented normal development. The high activity of the FSR alevins could in the same way cause an energy deficiency, and, further, a lack of morphological development, which could be a factor in first feeding mortality.

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Factors Affecting Variability of Trapnet Catches

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We summarized the literature relating to sampling characteristics of trapnets, and examined the variability of trapnet catches from Long Point Bay, Lake Erie. In Long Point Bay the frequency distributions of numbers of fish caught per trapnet lift were very skewed, peaking at zero for all species. Standard deviations of raw catches of even the most commonly taken species (*Ambloplites rupestris*, *Perca flavescens*, *Aplodinotus grunniens*) were high, about twice as large as their means. From 50 to 65% of the variability of transformed catches could be attributed to differences in soak time, sampling location, season, and year. Precision of estimating abundances of fish from catch-per-effort data is low for trapnets as well as for other sampling gear. Our fishing effort of nine trapnet lifts per sampling design cell sufficed to estimate, with 95% confidence, geometric mean catches in Long Point Bay to within a factor of 2 of their true values. To estimate them to within 20–25% would have required about 100 lifts. Regarding possible future changes of abundance, it would take 3 yr of observation to establish statistical significance of a decrease of arithmetic mean catches to half the levels observed in 1971–78.

Les auteurs résument les données publiées sur les caractéristiques d'échantillonnage de parc en filet et examinent la variabilité des captures réalisées à l'aide de cet engin dans la baie Long Point (lac Érié). À cet endroit, les distributions des fréquences numériques des poissons capturés par un parc étaient très asymétriques, atteignant un sommet à zéro pour toutes les espèces. Les écarts-types des prises brutes des espèces les plus communes (*Ambloplites rupestris*, *Perca flavescens*, *Aplodinotus grunniens*) étaient élevés, c'est-à-dire environ deux fois leur moyenne. De 50 à 65 % de la variabilité des prises transformées peuvent s'expliquer par les différences relatives à la période de mouillage, l'endroit d'échantillonnage, la saison et l'année. La précision de l'estimation du nombre de poissons à partir des données sur les prises par unité d'effort est faible pour les parcs en filet et d'autres engins d'échantillonnage. Un effort de pêche totalisant neuf mouillages de parcs en filet par cellule de plan d'échantillonnage a suffi pour calculer, à une limite de confiance de 95 %, la moyenne géométrique des prises dans la baie Long Point en deçà d'un facteur de 2 de leurs vraies valeurs. Une estimation se rapprochant de 20–25 % aurait requis environ 100 mouillages. Quant aux variations futures possibles de l'abondance, 3 années d'observation seraient nécessaires pour établir une signification statistique d'une baisse de la moyenne arithmétique des prises jusqu'à la moitié des taux observés de 1971 à 1978.

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Large weirs and pound nets have long been used to catch fish, especially migrating fish, in many parts of the world (von Brandt 1972). Trapnets were developed in the Great Lakes in the late 1800s and have since replaced most pound nets in the commercial fisheries of that area (e.g. Van Oosten et al. 1946; Langlois 1954). They are easier to use and more adaptable to different water depths and bottom conditions, since they are covered on top and do not require stakes to hold them in place.

Fyke nets catch fish in a similar fashion, but are (usually) smaller and lighter in construction, and are used in shallower water. They differ structurally in that fyke nets are held open by series of hoops, whereas trapnets are held open by tension between floats and weights, and between opposing anchor lines. The only rigid parts of a trapnet are a wooden pole and a metal pipe used to spread the top and bottom of the end that is lifted.

Trapnets are often used in fisheries research in North America, where in appropriate situations they give as good samples as other fishing gear do (e.g. Forney 1961; Yeh 1977). Still, variability among trapnet catches needs to be considered whenever they are used to compare or to estimate abundances of fish.

We have seen a few reports on variation of trapnet catches with location or season (e.g. Forney 1961), on selectivity of trapnets toward different sizes or species of fish (Latta 1959; Grinstead and Gomez 1972; Laarman and Ryckman 1982), and on relation of their catch to soak time (interval between lifts) (Van Oosten 1935; Patriarche 1968; Grinstead 1970). To these can be added some relevant studies with pound nets (Meyer and Merriner 1976), fyke nets (Schumacher and Eschmeyer 1943; Hansen 1944; Kelley 1953; Ryan 1984), wire mesh fish traps

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(Bagenal 1972; Munro 1974; Craig 1975), and even lobster traps (Austin 1977), but, still, too little has been published to allow a synthesis of the sampling characteristics of trapnets. As a step toward that end we outline what is known of the subject, and report our analysis of the magnitude and main sources of variability in catches made during 7 yr of trapnetting in Long Point Bay, Lake Erie.

Methods

The Ontario Ministry of Natural Resources has used trapnets and other gear to sample fish in Long Point Bay, Lake Erie, each summer since 1971, except in 1979. The methods and preliminary results of the trapnet study have been described by J. R. M. Kelso, G. C. Teleki, and others in the Ministry's internal reports.

We analyzed the 1971–78 catch data. However, as the sampling design was changed in 1973, we omitted all data from that year and did most analyses separately for 1971–72 and 1974–78, limiting each statistical test to the data most suited to it. Our analyses followed those of the Long Point Bay larval fish data, and some of the statistical considerations are explained in more detail in that report (Hamley et al. 1983).

Nets

Langlois (1954) described the operation of commercial trapnets in Lake Erie, and Crowe (1950) and Beamish (1973) detailed the construction and use of small trapnets for research. The nets used in the Long Point Bay study were of the type used in commercial fishing, made of black polypropylene twine, and with leaders 60–150 m long set at right angles to shore. Their pots ranged from 2.4 to 3.7 m in width, but most had the same mesh size, 5.7 cm stretched measure.

Locations

Long Point Bay is on the north side of Lake Erie, in the lee of a 35-km-long sandspit called Long Point. Trapnetting was done in "Nanticoke" and "western" sampling areas of that bay (Fig. 1). The former area is a 17-km-long stretch of exposed north shore, with much rocky bottom and little vegetation except attached green algae *Cladophora*. The latter area is sheltered from the predominantly westerly winds, with mainly sandy bottom, and facing an extensive shoreline marsh along Long Point.

About 40 different sampling sites were used in 1971–74, 61% of the sets being made in the Nanticoke and 39% in the western area. We omitted some of those sites and pooled others to give the 10 broader sampling locations shown in Fig. 1 to achieve adequate sample sizes for analysis and to facilitate comparisons with the 1975–78 data. Starting in 1975, sampling was discontinued in the western area and limited to six sites in the Nanticoke area, one in each of the locations WBP to SEL.

Sampling Scheme

In most years, trapnetting was done from late April to late October. To achieve sufficient sample sizes we grouped sampling (lifting) dates into four "seasons": spring (Apr. 1 – May 31), early summer (June 1 – July 19), late summer (July 20 – Aug. 31), and fall (Sept. 1 – Oct. 31).

In 1971–72 the nets were moved from site to site every few days, but in 1974–78 they were left in place for the season

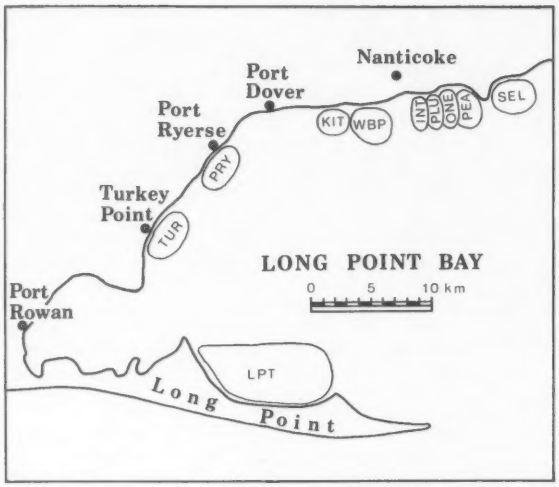

FIG. 1. Long Point Bay showing the Nanticoke (KIT to SEL) and western (PRY, TUR, and LPT) sampling locations.

except for occasional cleaning. The sampling design called for lifting nets daily in 1971–72 and twice a week in 1974–78, but in fact the average soak times were longer:

Year	1971	1972	1974	1975	1976	1977	1978
Soak time (d)	1.8	2.5	5.0	4.5	4.7	5.1	6.9

Most of the fish caught were released alive, in 1971–72 at the capture sites but thereafter at 100 m away from the capture sites, to avoid immediate recapture.

Different sizes of nets were used in different years and at different depths. In 1971–72 two nets were set at each sampling site, a 2.4-m (pot size) net closer to shore in 3–6 m of water and a 3.7-m net further out in 5–12 m of water, sometimes more than 1 km from shore. In 1974–78 only one net was set at each site, corresponding to the shallower sets of the earlier years. A 3.1-m net was used at ONE and 2.4-m nets at the other sites.

Selection of Data

In assessing the influence of sample size on precision of estimating mean catches, we used all six sites fished in 1976–78 (619 trapnet lifts). In assessing the effects of sampling variables (soak time, location, etc.) on catches, we used locations KIT, WBP, INT, and SEL-plus-PEA (173 lifts) from the Nanticoke area and all three locations (139 lifts) from the western area in 1971–72 and, in a separate analysis, locations WBP, PLU, and ONE (534 lifts) from the Nanticoke area in 1974–78. In assessing our ability to detect possible future changes from the 1971–78 levels of fish abundance, we used all sites from the Nanticoke area in 1974–78 (912 lifts) and the corresponding

sites in 1971–72 (74 lifts, not using the 3.7-m nets which were set in deeper water).

Statistical Analysis of 1971–78 Data

Frequency distributions of the numbers of fish caught were very skewed: while some lifts caught hundreds of fish, the most frequently recorded catch for even the commonest species was "zero." Although 82% of the lifts caught rock bass (*Ambloplites rupestris*), there were more lifts with no rock bass than with 1 or 2 or 3, etc., of them.

We calculated the precision of estimating mean catches of rock bass and yellow perch (*Perca flavescens*) in relation to the number of trapnet lifts per sampling design cell (same location, season, and year). Because of the skewed distributions of the raw numbers of fish caught, we did this in terms of geometric means of catch-plus-one-fish per lift. This is inconvenient as a descriptor of abundance, but suffices to indicate the attainable level of precision. For the two species mentioned, the frequency distributions of $\log (X + 1)$-transformed numbers of fish caught per lift were reasonably close to normal, so we calculated 95% confidence intervals for arithmetic means of the $\log (X + 1)$ data in the usual way. By taking antilogarithms, we then transformed those results to 95% confidence intervals of geometric means of the untransformed $(X + 1)$ data. (Note that subtracting 1 from our final results would not give the correct confidence intervals of geometric means of untransformed catches.)

In assessing the effects of sampling variables on catches, we used the 1974–78 data (the longest set of consistent observations) for analysis of main and interaction effects of the design variables location, season, and year and for testing the effect of soak time as a covariate. We used the 1971–72 data to examine additional information collected in the early years: the effects of setting at two different water depths and at western as well as at Nanticoke locations, and of shorter soak times.

Twelve species or pairs of species of fish were caught often enough to be analyzed separately (see Table 1). Of these, rock bass were caught often enough in all years, and freshwater drum (*Aplodinotus grunniens*) and yellow perch often enough in 1971–72 and 1974–78, respectively, for transformation of data into approximately normal distributions by recoding the observed catches to normal deviates according to their relative cumulative frequencies. After such transformations, we performed analyses of covariance (ANCOVA) on those data and on the total catches. (A log-transformation would probably have served as well, since for those three species the means and standard deviations of the numbers of fish caught per lift were approximately proportional.)

The data on the other nine species or pairs of species contained too high proportions of zero catches to be transformed into approximately normal distributions. Therefore, instead of analyzing the numbers of those fish caught per lift using ANCOVA, we analyzed the proportions of lifts that caught at least one (as opposed to none) fish of the kind in question, using the log-linear model multiway frequency classification analysis (Dixon and Brown 1979). (Soak time, which was included as a covariate in the ANCOVAs, was not considered here.) For comparison, we also analyzed the data on the first three species in this way.

Detection of Possible Future Changes

To assess our ability to detect possible future changes from the abundances of fish observed during the 1970s, we examined the year-to-year variability in two indices of abundance: mean number of fish caught per trapnet lift, and percentage of lifts that catch at least one fish of the species in question. Based on the 7 yearly means and the 7 yearly percentages observed in 1971–78, we used *t*-tests to estimate critical lower and upper limits within which future yearly means and percentages are expected to lie ($P = 0.05$ for one-tailed tests, $P = 0.10$ for two-tailed tests), if the abundances remain at the 1971–78 levels. We did this for observation in 1 future yr and for the average of observations in 3 or 10 future yr.

Before applying the *t*-tests we transformed the yearly means logarithmically, because in the case of some species the frequency distributions of raw catches per lift, even when averaged by year, were too skewed. For example, if the untransformed yearly catches were used in the analysis, a complete disappearance of white bass (*Morone chrysops*) or white sucker (*Catostomus commersoni*) for 5 yr could not be considered statistically significant.

In calculating the yearly proportions of trapnet lifts that catch at least one fish of the species in question, we used a formula that reduces the bias due to small sample size:

$$p = (f + \tfrac{1}{4})/(n + \tfrac{1}{2})$$

where p = the corrected proportion, f = number of non-zero catches, and n = number of lifts. We then transformed these yearly proportions to arcsine $(2p - 1)$. The raw yearly proportions were less variable and more normally distributed than the raw yearly catches per lift, but even so, a transformation was needed to improve the critical limits for 1 yr of future observation. For 3 or more yr, raw data would have given practically the same results as the arcsine-transformed data did.

To make our results easier to interpret we expressed them (see Table 6) as the raw catches per lift and the raw percentages of lifts that correspond to the critical lower and upper limits estimated for the log- or arcsine-transformed data. These retransformations to original units are not mathematically accurate, but are close enough to indicate approximate critical limits for the raw data.

Results and Discussion

The most commonly taken species in Long Point Bay was rock bass, followed by yellow perch and freshwater drum (Table 1). Quillback (*Carpiodes cyprinus*) were also caught in large numbers in 1971–72 when the LPT location was fished.

As shown in Table 1, standard deviations of the catches of even these commonly taken species were about twice as large as their mean values. Much of this variation was due to differences among soak times, sampling locations, seasons, and years. In the ANCOVAs on rock bass, 50–53% of the observed variability of normally transformed catches could be attributed to these four factors (compare "explained" and "total" SS in Table 2). In the ANCOVAs on yellow perch, freshwater drum, and total catch (not shown), these factors accounted for 54–65% of the variability.

Sample Size

Table 3 shows the 95% confidence intervals of mean catches of rock bass and yellow perch taken at a particular time and place in Long Point Bay. With the average of nine trapnet lifts that were made per sampling design cell (same location, season, and year), the confidence intervals spanned from about half to

TABLE 1. Species of fish caught most commonly in the Long Point Bay trapnets.

Species	Percentage of lifts that caught fish		Number of fish caught per lift (mean ± SD)	
	1971–72	1974–78	1971–72	1974–78
Rock bass *Ambloplites rupestris*	82	82	11.7±21.4	12.7±23.1
Yellow perch *Perca flavescens*	56	86	5.9±20.2	8.9±16.1
Freshwater drum *Aplodinotus grunniens*	80	46	20.6±40.5	3.1±8.7
Quillback *Carpiodes cyprinus*	32	15	23.5±132.4	0.4±1.6
White crappie *Pomoxis annularis* / Black crappie *P. nigromaculatus*	23	34	0.7±2.3	1.9±5.5
White sucker *Catostomus commersoni*	60	31	3.5±6.6	1.2±3.8
Smallmouth bass *Micropterus dolomieui*	40	28	2.0±4.9	1.0±3.4
White bass *Morone chrysops*	40	20	3.4±10.2	0.8±3.9
Pumpkinseed *Lepomis gibbosus* / Bluegill *L. macrochirus*	31	13	3.7±12.1	0.6±3.2
Carp *Cyprinus carpio* / Goldfish *Carassius auratus*	30	14	1.1±4.1	0.3±1.1
Yellow bullhead *Ictalurus natalis* / Brown bullhead *I. nebulosus*	15	13	1.0±7.9	0.3±1.0
Channel catfish *I. punctatus*	32	10	1.9±5.7	0.2±0.6
Other species	53	25	5.3±26.6	0.7±2.0

about double the mean catches. If these results are typical of sampling in other waters as well, one cannot get much more precise estimates of fish abundance with a reasonable amount of fishing effort. We would have needed some 100 lifts to be 95% certain of estimating the mean catches to within 20–25% of their true values.

As our trapnets were set 1.5 km or more apart and off shore, we do not think that they interfered with each others' catches. But in cases where sample sizes are increased by setting nets too close together, competition between different nets for capture of same fish will add another source of variability to the catch-per-effort data. In such cases, by analogy with competition between hooks on a longline (Hamley and Skud 1978), we would expect the catches to be reduced but not in proportion to the reduction of distance between nets.

Selectivity

We could not account for the effects of selectivity from our data, because in many years too few fish were measured to allow estimating their size–frequency distributions. However, we know that selectivity can bias mean catches. The smallest species of fish, such as emerald shiners (*Notropis atherinoides*), which were the most numerous fish taken by shoreline seining in Long Point Bay, or the young of any species, are not caught in ordinary trapnets because they escape through the meshes. Thus, the species and sizes of fish that are taken depend partly on the nets' mesh size (Van Oosten et al. 1946; Grinstead and Gomez 1972; Meyer and Merriner 1976; Craig 1980).

Furthermore, trapnet catches do not fully reflect even the relative abundances of those kinds of fish that are retained by the mesh (Schumacher and Eschmeyer 1943). Fish of some species, and fish of one sex or of larger size within a species, may behave in ways that make them more vulnerable to trapnets (Latta 1959). Since behavior can vary with the season, selectivity may do so also (Forney 1961).

Latta (1959) and Laarman and Ryckman (1982) have estimated relative selectivity curves ($\hat{s}_j$) of trapnets to rock bass and some other species of fish in a number of Michigan lakes by

$$\hat{s}_j = R_j/M_j$$

where M_j = number of marked fish of size class j released during a trapnetting study and R_j = the number of them recaptured in that same study. In most species, larger individuals were more likely to be caught.

Hamley and Regier (1973) estimated an absolute selectivity curve of trapnets to walleye (*Stizostedion vitreum*) in a small northern Ontario lake by

$$\hat{s}_j = R_j/C_j$$

where R_j = number of trapnet-marked fish among the C_j fish of size class j caught in gillnetting that followed the trapnetting. The trapnets, which were fished in spawning areas in May, caught over 70% of the walleye over 55 cm long in the lake, but only 10% of the 30-cm-long ones. Most of the catch were males which stay longer on the spawning grounds.

Soak Time

On the average, the 1971–72 catches in Long Point Bay examined by us (rock bass, freshwater drum, total catch) increased approximately in proportion to soak times of 1, 2, and 3 d, but not beyond. The results from 1974–78, when soak times were longer, were less clear but indicated an increase in catches with soak times of up to 4 or 5 d. The effect of soak time was statistically significant ($P < 0.05$) in all ANCOVAs except the one on yellow perch (Table 2).

Elsewhere, Van Oosten (1935), Hansen (1944), and Grinstead (1970) have shown that trapnet catches generally increase with time, but not proportionally. Progressively fewer fish are added on each succeeding day. This is partly because, although fish may not be alarmed by being confined in a trapnet (Rutecki et al. 1983), many of them will escape in time and the rate of escape can depend on the species. This was illustrated in an

TABLE 2. ANCOVA of normally transformed catches of rock bass in Long Point Bay.[a]

Source of variation	df	SS	MS	*F*	*P*
		1971–72			
Covariates					
Year	1	0.06	0.06	0.11	0.736
Depth	1	21.85	21.85	43.27	<0.001
Soak time[b]	1	12.37	12.37	24.49	<0.001
Main effects					
Location (L)	6	39.42	6.57	13.01	<0.001
Season (S)	3	36.35	12.12	23.99	<0.001
Interaction					
L × S	18	43.75	2.43	4.81	<0.001
Explained[c]	30	159.59	5.32	10.53	<0.001
Residual	281	141.91	0.51		
Total	311	301.50	0.97		
		1974–78			
Covariate					
Soak time[b]	1	2.45	2.45	4.67	0.031
Main effects					
Location (L)	2	20.19	10.09	19.25	<0.001
Season (S)	3	78.71	26.23	50.15	<0.001
Year (Y)	4	49.29	12.32	23.49	<0.001
Interactions					
L × S	6	41.66	6.94	13.24	<0.001
L × Y	8	42.52	5.31	10.13	<0.001
S × Y	12	29.79	2.48	4.73	<0.001
Explained[c]	36	259.07	7.19	13.72	<0.001
Residual	497	260.70	0.53		
Total	533	519.77	0.98		

[a]In similar analyses on freshwater drum in 1971–72, yellow perch in 1974–78, and total catch in 1971–72 and 1974–78, only the yellow perch *F*'s for soak time and L × S were nonsignificant ($P > 0.05$); all others had $P \leq 0.001$.

[b]Soak time data were coded nonlinearly for this analysis.

[c]Because the number of lifts varied among the sampling design cells, "explained" SS does not equal the sum of the SS above it.

experiment by Patriarche (1968) who marked trapnetted fish and returned them into the nets. All of his original pumpkinseed (*Lepomis gibbosus*) and largemouth bass (*Micropterus salmoides*), and smaller percentages of other fish, escaped within 3 d. Thus, the species composition as well as the number of fish caught can be affected by soak time (Grinstead 1970).

Munro (1974) found that when wire-mesh traps were left soaking on Caribbean coral reefs, each day about the same number of new fish entered them and about the same percentage of the ones inside escaped. The catches increased asymptotically for a week or more until the numbers escaping per day equalled the numbers entering.

Clearly, unless soak time is standardized, neither the number of lifts nor the number of days fished can be expected to be proportional to the numbers of fish caught, and neither can be relied on as a good measure of fishing effort. Munro (1974) and Austin (1977) have suggested ways to adjust the measure of trap fishing effort to account for unequal soak times, but because of the large variances of trapnet catches, such remedial measures are of limited value.

TABLE 3. Effect of sample size on precision of estimating rock bass and yellow perch abundances at a particular time and place in Long Point Bay (geometric means and 95% confidence limits of the observed catch-plus-one-fish per trapnet lift in the Nanticoke sampling area in 1976–78).

Number of lifts	Rock bass			Yellow perch		
	Lower limit	Mean	Upper limit	Lower limit	Mean	Upper limit
9	2.6	5.9	13.7	2.7	5.5	11.0
20	3.4	5.9	10.4	3.4	5.5	8.8
50	4.2	5.9	8.5	4.1	5.5	7.4
100	4.6	5.9	7.6	4.4	5.5	6.8

Location

In Long Point Bay, catches of the commonly taken species varied several-fold between the sampling locations (Table 4). The greatest difference was between LPT and the other locations: total catches at LPT were twice as large as anywhere else, due to large catches of quillback. The among-location variability was much larger in quillback than in rock bass or yellow perch.

The effect of location on catch was statistically significant in all ANCOVAs for the three most commonly taken species (Table 2), and in most log-linear model comparisons for the other nine species or pairs of species (Table 5). Comparison of Tables 2 and 5 shows that although the two statistical methods generally gave similar results, they did not always do so. Notably, the numbers of rock bass caught varied greatly between the sampling locations ($P < 0.001$), but the percentages of lifts that took at least one rock bass were consistently high at all locations. Because the percentage of lifts that catch fish depends on the degree of clustering of fish as well as on their numbers, the two measures of abundance do not necessarily vary in unison.

Water depth or its correlate, distance from shore, also had a significant effect on the catches (Tables 2 and 5) (the results cannot be attributed to the use of two net sizes.) In 1971–72 when nets were set at two depths at each sampling site, the ones further out in 5–9 m of water caught twice as many fish as the ones closer to shore in 3–6 m of water. The deeper set nets caught more freshwater drum, quillback, white bass, carp (*Cyprinus carpio*), and goldfish (*Carassius auratus*), while the shallower set nets caught more rock bass, yellow perch, smallmouth bass (*Micropterus dolomieui*), and sunfishes (*Lepomis* spp.).

Large differences in catches between sampling sites or depths have been found elsewhere (e.g. Schumacher and Eschmeyer 1943; Van Oosten et al. 1946) as well as in Long Point Bay. In many cases they may be explainable by habitat preferences of the fishes, but it is also possible that vulnerability to capture is affected by habitat, in particular, by extent of nearby vegetation or other cover, and by presence or absence of currents.

Season

At the Nanticoke sampling sites, catches of rock bass, yellow perch, freshwater drum, and all species combined were highest in the spring, whereas catches of sunfishes, crappies (*Pomoxis* spp.), and some other species were highest in late summer and

TABLE 4. Arithmetic mean numbers of fish caught per lift in Long Point Bay at the locations used in the ANCOVAs.

Location	Rock bass	Yellow perch	Freshwater drum	Quillback	Total catch
			1971		
SEL, PEA	4.1	3.4	20.3	0.6	48.7
INT	8.3	1.0	7.4	0.6	41.0
WBP	6.0	1.5	9.9	1.0	44.6
KIT	4.0	2.1	3.8	0.9	30.3
PRY	19.6	0.8	8.7	0.7	39.7
TUR	50.6	2.3	16.7	14.8	111.0
LPT	6.6	0.6	23.4	128.1	239.6
			1972		
SEL, PEA	5.9	8.3	15.4	0.4	37.1
INT	13.1	10.3	43.0	0.1	76.3
WBP	6.5	4.4	18.4	0.7	37.9
KIT	8.3	4.6	26.2	0.2	49.8
PRY	20.1	6.1	31.5	0.2	67.0
TUR	27.2	4.4	30.1	1.1	73.8
LPT	3.7	22.7	11.0	78.9	142.1
			1974		
ONE	17.7	8.1	9.9	0.6	50.2
PLU	32.8	36.3	4.1	0.1	95.7
WBP	12.1	1.7	6.9	0.8	27.8
			1975		
ONE	9.7	4.0	6.2	0.4	25.6
PLU	10.1	4.9	0.4	0.0	16.9
WBP	2.4	3.1	0.1	0.0	6.7
			1976		
ONE	20.6	9.8	9.8	0.6	54.2
PLU	15.5	7.5	3.4	0.1	29.9
WBP	7.7	1.8	0.5	0.0	10.9
			1977		
ONE	10.1	9.0	7.6	0.5	34.5
PLU	30.0	31.9	1.4	0.1	73.5
WBP	18.7	4.9	0.4	0.1	26.7
			1978		
ONE	20.6	5.3	5.7	1.3	48.9
PLU	14.8	8.1	1.3	0.0	34.0
WBP	35.8	24.3	0.9	0.3	66.8

fall (Fig. 2). For most species these changes were statistically significant (Tables 2 and 5).

Such seasonal variations in trapnet catches are common, and may result from mortality, recruitment of a new year-class to catchable size, migrations of fish to and from the study area, or changes in catchability due to seasonal changes in fish behavior (Kelley 1953; Ryan 1984). The effect of behavior can be seen in Craig's (1975) and our data on perch, neither of which can be explained by seasonal migrations. Craig's catches of Eurasian perch (*Perca fluviatilis*) in wire-mesh traps increased toward the spawning season and then declined; this trend was seen in all parts of his lake. Our data from Long Point Bay show that trapnet catches of yellow perch declined in early summer (Fig. 2); yet those fish did not appear to leave the study area, as their catches in gillnets did not decline until the fall (Ministry of Natural Resources, unpubl. data).

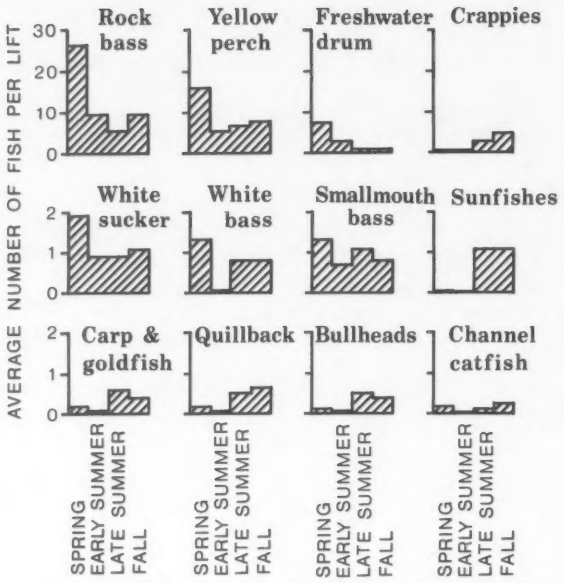

FIG. 2. Seasonal distribution of trapnet catches in the Nanticoke sampling area. (Note the different scale of the top row of histograms.)

Year

In Long Point Bay the yearly mean numbers of fish caught per trapnet lift varied 4- to 5-fold for the three most commonly taken species, and up to 30-fold for four less commonly taken kinds of fish (Fig. 3). Our other index of abundance, the percentage of lifts that caught at least one fish, was more stable: it varied less than 2-fold for the three most commonly taken species, and 2- to 5-fold for the other four. The year-to-year variations in total catch and in catches of individual species were in most cases statistically significant (Tables 2 and 5), but showed no consistent long-term trends (Fig. 3).

To help recognize trends that may emerge later, we established criteria of statistical significance for possible future changes from the 1971–78 catch levels, assuming that the same amount of fishing effort (about 200 lifts per year) is continued into the future (Table 6). For most of the species considered it would take about 3 yr of observation to establish $P \leq 0.10$ statistical significance of the change if the mean abundances decreased to the lowest or increased to the highest levels observed during 1971–78, i.e. if the mean numbers of fish caught per lift changed by about a factor of 2 from their recent levels (cf. Fig. 3). After a single year of observation, a change of that magnitude would be significant only at $P \leq 0.20$ (not shown in Table 6).

Interactions

We found significant location-by-season interactions in the catches of rock bass, freshwater drum, crappies, and smallmouth bass in Long Point Bay (Tables 2 and 5). Such findings suggest the possibility of seasonal along-shore migrations, and, indeed, mark–recapture studies have shown that rock bass and smallmouth bass from the Nanticoke area migrate each spring to spawn in the western parts of Long Point Bay (MacLean and Teleki 1977).

Seasonal inshore–offshore migrations have been reported for

TABLE 5. Log-linear model analysis of the Long Point Bay data showing statistically significant associations between catches (none versus some fish) and the following factors and their interactions: L = location, Y = year, D = depth, and S = season. $*P \leq 0.05$, $**P \leq 0.001$.

	1971–72					1974–78					
Species	L	Y	D	L×Y	L×D	L	Y	S	L×Y	L×S	Y×S
Rock bass			**				*	*		*	*
Yellow perch	*	**	*		*	**	*				
Freshwater drum	*		**			**	*	**	**		**
Quillback	**		**			**	*	*			**
Crappies	*	**		*		**		**		**	
White sucker	*			*		**	**	*			*
Smallmouth bass		**	**	*		**	**	**		**	*
White bass			*			**	**	**			**
Sunfishes	**	**	**			*	**	**			
Carp and goldfish	*		**			*	*	*	*		*
Bullheads	**	**				**	*	**	**		
Channel catfish	**					*	**	*			
Total catch	*		**			**	**	**	**		**

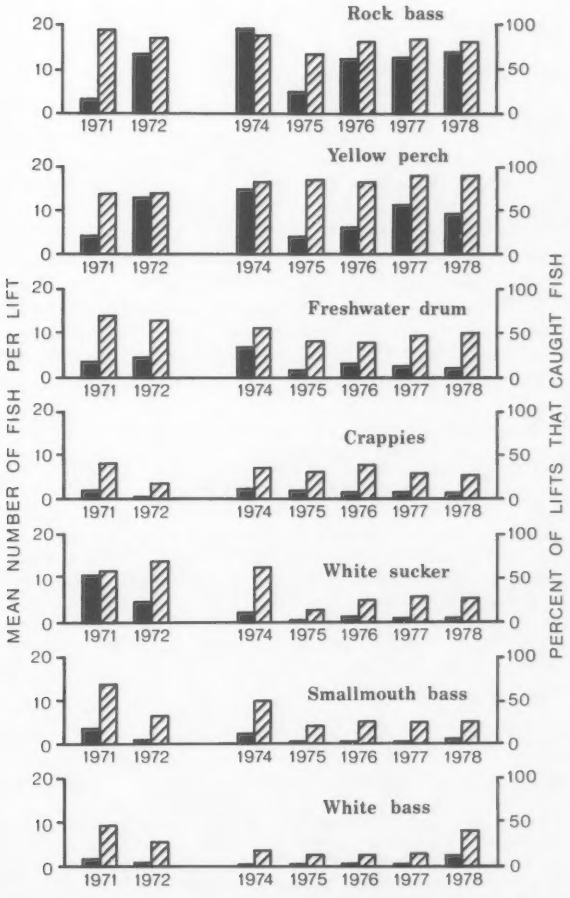

FIG. 3. Yearly abundances of fish in the Nanticoke sampling area: ■, arithmetic mean number of fish caught per trapnet lift; ▨, percentage of lifts that caught at least one fish of the specified kind.

many freshwater fishes (e.g. Dahlberg 1981), but were not apparent in our data even though a log-linear model analysis (not shown) indicated a significant season-by-depth interaction for quillback. Large numbers of quillback were caught in the deeper set nets in late summer and fall, but that was only at LPT and we do not know where those fish may have concentrated during the rest of the year.

Season-by-year and location-by-year interactions were significant in many cases (Tables 2 and 5) but were difficult to interpret. Some of them can be explained by inconsistencies in sampling; e.g. considering yellow perch at LPT (Table 4), most of the high 1972 catch was taken in the spring, whereas in 1971 when their catch was low the sampling was not started until the summer. On the other hand, we do not know why smallmouth bass were caught in greatest numbers during the spring in 1976 and 1978 versus during late summer in 1975 and 1977, or why catches of rock bass and yellow perch at WBP were so high in 1978 after having been low in the previous years (Table 4). Those results may reflect the effects of weather or of slightly different placement of the nets from one year to another.

We do not know how many of the season-by-year and location-by-year interactions would remain statistically significant if the year-to-year variations in sampling could be eliminated. This again shows the importance of standardizing the sampling design and methods.

Residual Variation

As noted earlier, much of the variation in the Long Point Bay catches (Table 1) was related to differences in sampling time and place. Catches from the same combination of location, season, and year showed standard deviations only half as large as those in Table 1, roughly equal to mean catches in case of the most commonly taken species. In the ANCOVAs such residual, or unexplained, variation accounted for 35–50% of the total sums of squares (Table 2).

We suspect that some of this variability was due to influence of weather on movements and catchability of fish. Winds, for example, can quickly change underwater conditions in the

TABLE 6. Detecting possible changes from the 1971–78 abundances of fish in Long Point Bay. Critical lower and upper limits for the arithmetic mean numbers of fish caught per trapnet lift and for the arithmetic mean percentages of lifts that catch at least one fish of the kind in question in 1, 3, and 10 yr of future observation. $P = 0.05$ for one-tailed and $P = 0.10$ for two-tailed tests. Calculated from the yearly means and percentages shown in Fig. 3.

Species	1 yr		3 yr		10 yr	
	Lower	Upper	Lower	Upper	Lower	Upper
	Number per lift					
Rock bass	3.1	33.9	4.6	22.6	6.0	17.4
Yellow perch	2.8	22.5	4.0	15.8	5.0	12.6
Freshwater drum	1.3	7.8	1.8	5.8	2.1	4.7
Crappies	0.4	6.3	0.6	3.9	0.8	2.8
White sucker	0.2	16.3	0.4	7.8	0.7	4.8
Smallmouth bass	0.3	4.6	0.5	2.9	0.6	2.2
White bass	0.1	4.1	0.2	2.2	0.3	1.5
	Percentage of lifts					
Rock bass	66	97	73	94	77	91
Yellow perch	64	94	70	91	74	88
Freshwater drum	30	74	38	67	42	62
Crappies	19	48	23	42	26	39
White sucker	6	82	15	70	23	60
Smallmouth bass	8	70	16	59	22	51
White bass	4	54	9	44	14	37

relatively shallow Long Point Bay, setting up seiches and increasing turbidity by stirring bottom clays.

Conclusion

We have shown, from an overview of literature and our own analysis of data from Long Point Bay, that both the variance and the bias components of trapnet catch variability are substantial. One should not expect to get very accurate estimates of fish abundance from such data. This, however, is not just a problem with trapnets but with catch-per-effort data in general, and as far as we know, applies to other kinds of fishing gear as well (e.g. Grosslein 1971; Bagenal 1972; Craig and Fletcher 1982; Vaughan and Van Winkle 1982; Hamley et al. 1983).

A large variance component is an unavoidable consequence of the very clustered distributions of fish in lakes; it can be made even larger by changes of catchability with season and weather, and, in multiyear studies, by variations of incoming year-class size. Biases can arise from inconsistencies in sampling technique, from comparing fish populations of different years or areas where their size compositions differ, and from mixing data from different seasons or habitats where fish may react differently toward the nets.

These problems should be considered at the planning stages of each new trapnetting study to ensure a predictable degree of success. If previous trapnet catch records are available from the same or a similar lake, the variance in them can be used to predict how many "replicate" lifts will be needed in a comparison of abundances between locations, or how many years of observation will be needed in a "before and after" study of environmental impacts.

Most of the sampling biases can be alleviated by standardizing the nets, fishing methods, and sampling design, but usually the effects of size selectivity cannot be avoided. Fish tend to appear more abundant where their average size is larger. In some cases this effect may be corrected on the basis of published trapnet selectivity curves, but unfortunately only a few such curves exist and the extent of their applicability to other waters and trapnet designs has not been established. When a correction cannot be made, the best one may be able to do is to estimate fish abundances separately by size classes (Latta 1959).

When sample sizes are adequate and sampling design and analysis of data account for catch variability, trapnet catches can provide a useful index of fish abundance. Thus, Ryan (1984), who fished with fyke nets in two Newfoundland lakes, found that seasonally adjusted catches of brook trout (*Salvelinus fontinalis*) and young Atlantic salmon (*Salmo salar*) correlated well with mark–recapture estimates of their population densities.

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Responses of *Isonychia bicolor* to Alkaline pH: An Evaluation of Survival, Oxygen Consumption, and Chloride Cell Ultrastructure

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The toxicity of alkaline pH to the mayfly, *Isonychia bicolor*, was evaluated in field and laboratory artificial stream bioassays, respiration analyses, and transmission electron microscope studies of chloride cell ultrastructure. In continuous-exposure, 96-h bioassays, field and laboratory LC50 values ranged from pH 9.54 to 10.37, respectively. While intermittent pH bioassays involving 8- or 4-h exposures per day failed to reduce alkaline pH toxicity, 1-h intermittent exposures were less toxic ($P < 0.05$) than continuous exposures. Acute (4-h) exposures to lethal (pH 11.0) and sublethal (pH 10.0) levels caused reductions ($P < 0.05$) in oxygen consumption relative to that at pH 8.0. Oxygen consumption at pH 11.0 was greater ($P < 0.05$) than that at pH 10.0. Coniform chloride cells continuously exposed to pH 11.0 for 96 h accumulated fluid near the porous plate, and these fluid accumulations displaced cytoplasm from the apical region of the cell complexes. Chloride cells intermittently exposed to pH 11.0 (1 h per day for 96 h) appeared similar to those continuously exposed to pH 11.0, indicating that the damaging effects of 1-h exposures exceeded the rehabilitory effects of daily, 23-h recovery periods. Structural recovery (95%) occurred within 8 d following the cessation of intermittent exposure to pH 11.0.

On a évalué la toxicité d'un pH alcalin pour l'éphémère, *Isonychia bicolor*, à l'aide de titrages biologiques en laboratoire et sur le terrain, d'analyses de la respiration et d'études, au microscope électronique à transmission, de l'ultrastructure des cellules à chlorures. Au cours d'expositions continues de 96 h en laboratoire et sur le terrain, les valeurs de la CL50 du pH ont varié de 9,54 à 10,37 respectivement. Des bio-analyses intermittentes du pH comprenant des expositions de 8 h ou de 4 h par jour n'ont pas réduit la toxicité du pH alcalin, mais des expositions intermittentes de 1 h étaient moins toxiques ($P < 0,05$) que des expositions continues. Des expositions intenses (4 h) à des niveaux létaux (pH 11,0) et sublétaux (pH 10,0) ont entraîné une baisse ($P < 0,05$) de la consommation en oxygène par rapport à celle à un pH 8,0. À un pH 11,0, la consommation en oxygène était plus élevée ($P < 0,05$) qu'à un pH 10,0. Les cellules à chlorures coniformes exposées continuellement à un pH 11,0 pendant 96 h ont accumulé du fluide près de la surface poreuse; cette accumulation a déplacé le cytoplasme de la région apicale des complexes cellulaires. Les cellules à chlorures exposées par intervalles à un pH 11,0 (1 h par jour pendant 96 h) étaient d'apparence semblable à celles qui étaient continuellement exposées à un pH 11,0, ce qui révèle que l'incidence négative d'expositions de 1 h dépasse l'incidence des périodes quotidiennes de désintoxication d'une durée de 23 h. Au niveau structural, la récupération (95 %) a eu lieu en deçà de 8 d suivant la fin de l'exposition intermittente à un pH 11,0.

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In many regions of the United States, power plants generating electricity utilize coal which substantially increases the pH of river water used to precipitate fly ash particles produced in the combustion process. Although the precipitates are allowed to fall out of suspension in settling basins, subsequent releases of highly alkaline supernatant water into nearby streams result in conditions that are stressful to the indigenous biota. Specht et al. (1984) observed that mayflies became less abundant in a stream system receiving fly ash effluents that intermittently approached pH 9.5. Laboratory analyses revealed that the mayfly, *Stenonema pudicum*, was highly sensitive to alkaline pH; the 96-h LC50 was only pH 9.5 (Specht et al. 1984). This study emphasized the need for additional research regarding the effects of constant and intermittent alkaline pH effluents associated with power plant installations. Due to the paucity of relevant information in the literature, the limitations of alkaline pH regulations set forth by regulatory agencies to maintain the environmental integrity of sensitive aquatic insect communities are impossible to evaluate at present.

Unlike stream acidification where a considerable amount of information exists in the literature (Roback and Richardson 1969; Haines 1981), alkaline pH disturbances have received little attention, especially regarding their impact upon aquatic invertebrates. In addition to Specht et al. (1984), studies dealing with the toxicity of alkaline pH to the freshwater shrimp, *Paratya curvirostris* (Shaw 1981), and the osmoregulatory responses of stoneflies to reduced hydrogen ion concentrations (Lechleitner 1982) represent the existing evaluations of the toxicity of alkaline pH to aquatic macroinvertebrates.

The purpose of this study was to evaluate the effects of alkaline pH on the widely distributed mayfly, *Isonychia bicolor*. A series of field and laboratory bioassays was conducted to assess alkaline pH toxicity under a variety of water quality conditions. Since industrial discharges can be regulated for

release during noncritical periods (e.g. high-flow conditions or late night when diurnal fluctuations in pH due to photosynthetic uptake of carbon dioxide reach 24-h minima), tests were conducted under both constant and intermittent exposure regimes.

Based upon studies concerning the disruption of osmoregulation in fish exposed to acidic stress, Fiance (1978) hypothesized that reduced growth observed in the mayfly, *Ephemerella funeralis*, experiencing acid mine drainage might be explained by the utilization of energy resources for maintaining ionic balances. Similarly, we hypothesize that alkaline pH may disrupt osmoregulation and influence oxygen consumption in *I. bicolor*. Because changes in chloride cell structure have been shown to reflect osmoregulatory stress caused by extreme environmental salinities (e.g. Wichard et al. 1973), transmission electron microscopy (TEM) was utilized to evaluate ultrastructural changes in *I. bicolor* cells exposed to alkaline pH. Oxygen consumption by *I. bicolor* was monitored to assess the potential energy requirements of osmoregulation during acute exposures to elevated pH.

Materials and Methods

Isonychia bicolor is a bivoltine mayfly with spring and summer generations. One of 25 species recognized as members of the Oligonuriidae (McCafferty and Edmunds 1979), *I. bicolor* is primarily a filter-feeder, consuming particulate organic material in the 0.1- to 0.7-μm size range (Wallace and O'Hop 1979). Nymphs used in the study were collected from two adjacent riffle areas in Sinking Creek, VA, ~15 km from its confluence with the New River. Sinking Creek pH levels ranged from pH 6.8 to 8.5 from October 1981 through October 1983. All test results refer to experiments using the summer generation, although the winter generation was used in range-finding tests. Nymphs selected for use in the analyses ranged in length from 1 to 2 cm and ranged in weight from 2.245 to 23.060 mg ($\bar{x}$ = 8.713 mg; SD = ±6.281).

Bioassays

Laboratory bioassays were conducted in the Ecosystem Simulation Laboratory of Virginia Polytechnic Institute and State University, while field bioassays were conducted on the bank of the New River at the Glen Lyn Power Plant, Glen Lyn, VA. In static, 96-h laboratory bioassays, insects were placed in 2.5-L glass containers filled with 2.0 L of pH-adjusted dechlorinated tap water. These round containers were placed on magnetic stirrers to maintain current, and nymphs were held in fiberglass screen cages suspended above the magnetic stir bars. Common aquarium pumps maintained oxygen concentrations, and temperature levels were regulated by conducting the entire experiment in a large incubator equipped with fluorescent lighting to provide a 12L:12D photoperiod. Hydrogen ion concentrations were adjusted with NaOH every 8 h to prevent fluctuations in pH, and water in each container was completely renewed every 24 h to prevent the excessive accumulation of waste materials. Static test results were to be compared with those of flow-through systems which prevent the buildup of waste materials, supply fresh quantities of aerated water, and achieve a higher level of environmental realism. Field and laboratory flow-through experiments were conducted in oval, paddle wheel driven, artificial streams ~76 × 33 × 15 cm. These artificial streams received unaltered stream water pumped directly from the New River in the field tests, while municipal tap water, which is drawn from the New River before distribution to the town of Blacksburg, VA, was dechlorinated with activated charcoal for use in the laboratory tests. Water was delivered to each stream at a rate of 0.25 L/min, and wastewater exited at an equivalent rate through 10-cm-tall standpipes. Turnover time in the 12-L streams was 48 min. Laboratory test temperatures (20.0°C; range 19.0–21.0°C) were regulated with aquarium heaters placed in each stream, while field water temperature fluctuated according to variations in New River water temperature (mean 24.0°C; range 21.0–27.0°C). A 12L:12D photoperiod was maintained with fluorescent lighting in the laboratory bioassays; natural photoperiods (~14L:10D) occurred in field tests. Fisher pH meter/controllers continuously maintained the pH of each stream by activating peristaltic pumps that supplied NaOH held in 18-L glass carboys. Electrodes were standardized twice daily with pH 7.00 and pH 10.0 buffers. During all tests, pH levels remained within ±0.1 unit of the target concentration. Although no food was made available to nymphs in laboratory studies, algae and particulate organic matter entered the field system via river water.

Isonychia bicolor nymphs were randomly distributed among fiberglass screen holding cages until each experimental container held three cages of 10 insects. Organisms were acclimated to test conditions in their respective artificial streams for 24–48 h. Due to limited information on the nutritional requirements of the test species, bioassays were initiated within 24–48 h to prevent nutritional stress. In the continuous-exposure bioassays, pH was elevated to test levels within 15 min and maintained for 96 h. Nymphs exposed to intermittent pH conditions (1, 4, or 8 h/d for 4 d) were placed in their respective experimental streams, and pH was similarly elevated within 15 min and maintained for the duration of the exposure period. Immediately following each daily, intermittent exposure to alkaline pH, the insects and their respective cages were removed and placed in artificial streams held at ambient pH levels. Experiments were conducted with two replicate analyses so that a total of 90 insects was exposed to each of six experimental pH levels, which bracketed the 96-h LC50 and included 0 and 100% mortality. Toxicity was evaluated using probit analyses for computation of LC50 values and 95% fiducial limits (SAS Institute Inc. 1982). Because the insects in each test container were exposed to identical experimental conditions, data from all three cages per container were pooled, and the LC50 for each of the replicate analyses was calculated with 30 organisms per test level. Hydrogen ion concentrations were used in these analyses rather than pH. Statistical tests were based upon nominal pH values, since actual pH levels fluctuated within a narrow range above and below the target concentration (±0.1 pH unit).

Transmission Electron Microscopy

Specimens used in the TEM analyses were exposed to alkaline pH in laboratory artificial streams by the methods used in the bioassays. The following exposure regimes were used to evaluate the effects of constant and intermittent exposures of alkaline pH on *I. bicolor* coniform chloride cells: 96 h at pH 10.0; 96 h at pH 11.0; 1 h/24 h at pH 10.0 for 96 h; 1 h/24 h at pH 11.0 for 96 h; 1 h/24 h at pH 11.0 for 96 h + 23-h recovery period; 1 h/24 h at pH 11.0 for 96 h + 4-d recovery period; 1 h/24 h at pH 11.0 for 96 h + 8-d recovery period.

Thin sections of gills from abdominal segments 3–5, fixed with cacodylate-buffered osmium tetroxide, embedded in Spurr's resin, and poststained with uranyl acetate and lead

citrate, were examined and photographed with a transmission electron microscope.

Ultrastructural changes were evaluated at each exposure level by examining a minimum of 12 chloride cells. Changes in the density of the cytoplasm were estimated by determining the proportion of the cell composed of reference cell density. The extent of vacuole formation was evaluated by laying a grid over each micrograph to quantify the cross-sectional area of each vacuole. This value was expressed as a percentage of total cell area. The association of the plasma membrane and the porous plate was assessed by measuring the length of the plate with which the membrane was associated.

Oxygen Consumption

Oxygen consumption of *I. bicolor* was examined at pH levels 8.0, 10.0, and 11.0 because (1) normal metabolic rates were expected to be observed at pH 8.0, since this level approximated field conditions in Sinking Creek where the nymphs were collected, (2) partial lethality was expected at the LC10 level of pH 10.0, and (3) substantially different metabolic rates were expected at pH 11.0, since this level exceeded the 96-h LC50 value (pH 10.37) derived from preliminary bioassays.

Nymphs were transported to the laboratory in aerated creek water and held for 24–48 h at 18.0°C prior to testing. Field water temperatures at the time of collection ranged from 17.0 to 19.0°C. Oxygen consumption was measured manometrically with a Gilson differential respirometer (Gilson 1963). Filtered creek water was adjusted to the desired pH using NaOH, and 8.0 mL was transferred to each experimental flask. Respired carbon dioxide, which was liberated by agitating the flasks at a shaking speed of 52 oscillations/min, was absorbed with 300 μL of 20% KOH held on filter paper in the center wells of the reaction vessels. Fiberglass screens were placed in the flasks for nymphs to grasp during the experiment. Three reference flasks were used in each repetition to correct oxygen consumption measurements for microbial respiration, which varied from 0.0 to −3.18 μL oxygen/h. Oxygen consumption experiments were carried out until at least 60 observations were recorded per pH exposure level. Since measurable oxygen consumption values were observed with single *I. bicolor* nymphs, only one insect was placed in each experimental flask. This procedure prevented the calculation of average oxygen consumption, which lessens the natural variability of oxygen consumption data (by reducing the effects of outliers) and artificially results in better fitted regression models and R^2 values. Oxygen consumption values associated with organisms that expired at pH 11.0 were not included in the analysis because the exact time of death could not be determined. Consequently, the number of repetitions varied according to the number of insects that survived at the higher pH levels.

After a 1-h acclimation period, oxygen consumption was monitored for 3 h. Manometer readings were taken at the beginning and end of the exposure period and converted to yield average oxygen consumption per hour. Shorter exposure periods were not used to avoid the introduction of excessive experimental error from adjustments to small changes in pressure. Longer exposure periods were avoided to prevent changes in pH. The pH level of each flask was adjusted to within ±0.05 pH unit of the target concentration at the initiation of the test. During the experiment, pH levels declined 0.0–0.2 pH unit. Regression analyses (oxygen consumption vs. weight) were performed with the least squares method (Sokal and Rohlf 1969) for each experimental pH group.

Results and Discussion

Bioassays

The toxicity of alkaline pH to *I. bicolor* was greater under field bioassay conditions (Table 1); the LC50 values from field and laboratory artificial stream tests dealing with constant pH exposures (9.54 and 10.37, respectively) differed by 0.83 pH unit ($P < 0.05$). Because regression lines (mortality vs. pH) were not parallel and could not be compared using potency probit analyses, LC50 values were considered to differ at the 0.05 level when the 95% fiducial limits of one test failed to include the LC50 value of another test (Sprague and Fogels 1977).

Several hypotheses offer potential explanations for the differences in toxicity. Water quality parameters in the field and laboratory bioassays were remarkably similar except for hardness and Mg^{2+} levels, which were approximately twice as high in the field tests (Table 2). Total Ca^{2+} and Mg^{2+} levels (26.92 mg/L laboratory vs. 30.04 mg/L field) differed by 10%. Calcium ions, and to a lesser extent Mg^{2+}, have been demonstrated to affect the toxicity of H^+ to fish by many investigators (e.g. Oduleye 1975; Leivestad et al. 1976; McWilliams and Potts 1978; Pic and Maetz 1981; McDonald et al. 1983). For example, McDonald et al. (1983) observed that elevated levels of Ca^{2+} and Mg^{2+} reduced the toxicity of low pH and decreased osmoregulatory stress in rainbow trout (*Salmo gairdneri*). Although several mechanisms have been proposed to explain the effects of Ca^{2+} and Mg^{2+} on osmoregulation, the most plausible involves the binding of these ions at the pores of transport epithelia (see discussion in McDonald et al. 1983). At near-neutral pH levels, Ca^{2+} and Mg^{2+} are thought to bind near openings in the porous plate and regulate pore size. Under low pH conditions, H^+ attaches at these binding sites and displace the larger Ca^{2+} and Mg^{2+}, effectively increasing pore size. As a consequence of increased pore size, Na^+ is lost from the cells and osmoregulatory stress ensues. Although acidification enhanced the displacement of Ca^{2+} and Mg^{2+} from epithelial pores and resulted in substantial Na^+ losses from rainbow trout, elevated levels of Ca^{2+} and Mg^{2+} were observed to counteract the effects of acidification and prevent osmoregulatory stress (McDonald et al. 1983).

In our study, alkaline pH toxicity was enhanced under the increased Ca^{2+} and Mg^{2+} levels of the field tests. We suggest that increased Ca^{2+} and Mg^{2+} levels, in conjunction with reduced H^+ concentrations at elevated pH which enhanced the availability of epithelial binding sites, resulted in the saturation of epithelial binding sites. Consequently, the attachment of Ca^{2+} and Mg^{2+} at the pores under alkaline pH conditions may have induced osmoregulatory stress in *I. bicolor* by inhibiting the passive efflux of ions that normally occurs at the gill surface. Data are not available in the literature to compare *I. bicolor* responses with other insect species experiencing alkaline pH stress.

Variations in temperature regime could also have affected the ability of the nymphs to cope with alkaline pH stress. Laboratory water temperatures remained within 1° of the 20°C test temperature, showing no observable diurnal fluctuations. However, field water temperatures averaged 24.0°C, fluctuating

TABLE 1. Laboratory and field, 96-h alkaline pH bioassays with *I. bicolor*, expressed as LC50 values and their upper (U95% FL) and lower (L95% FL) 95% fiducial limits. In each bioassay, three repetitions were conducted using 30 insects per exposure level ($N = 90$).

Bioassay	L95% FL	LC50	U95% FL
Laboratory			
Static	10.06	10.33	10.58
Artificial stream			
Continuous pH exposure	10.29	10.37	10.45
8 h elevated pH/24 h	10.18	10.39	10.55
4 h elevated pH/24 h	10.33	10.53	10.71
1 h elevated pH/24 h	10.60	10.77	10.92
Field			
Artificial stream			
Continuous pH exposure	9.29	9.54	9.79
1 h elevated pH/24 h	10.34	10.48	10.62

TABLE 2. Mean water quality data for all alkaline pH bioassays using *I. bicolor* conducted at the Ecosystem Simulation Laboratory (Virginia Polytechnic Institute and State University) and at the Glen Lyn Field Laboratory.

Parameter	Ecosystem Simulation Laboratory ($n = 12$)	Glen Lyn Field Laboratory ($n = 6$)
Temperature (°C)	20.0 (range 19.0–21.0)	24.0 (range 21.0–27.0)
pH	7.96	8.51
Alkalinity (mg/L)	45.9	51.3
Conductivity (μS)	132.0	131.5
Hardness (mg/L as $CaCO_3$)	64.2	101.7
Ammonia (mg/L)	<0.050	0.069
Orthophosphates (mg/L)	0.052	0.032
Total phosphates (mg/L)	0.082	0.062
Nitrates (mg/L)	0.572	0.944
Sulfates (mg/L)	11.65	14.80
Na (mg/L)	5.43	5.77
Ca (mg/L)	22.79	21.63
K (mg/L)	1.41	1.27
Mg (mg/L)	4.13	8.41

from 21.0 to 27.0°C according to diurnal changes in solar radiation. It is probable that a mean difference of 4.0° could account for a change in toxicity of the magnitude observed between the two bioassays, as a 4° average difference represents a Q_{10} change of ~60%. Afternoon temperatures as high as 27°C could also have induced thermal stress, since the highest temperature recorded over a 2-yr period in Sinking Creek where the test specimens were collected was 24°C (Kondratieff 1982).

No differences ($P < 0.05$) were observed between continuous, 96-h exposures to high pH and those that lasted only 8 or 4 h/d (Table 1). While 50% of the test organisms expired at pH 10.37 in the constant pH bioassays, the LC50 values for 8- and 4-h intermittent tests were 10.39 and 10.53, respectively. Since survival under these intermittent exposure regimes failed to differ significantly from that observed under constant pH conditions, it seems that daily exposures to high alkaline pH lasting 4–8 h were as harmful to *I. bicolor* as 96-h continuous exposures. Presumably, the inability of mayflies to recuperate during the daily recovery periods accounted for these similarities in toxicity.

A substantial decrease in toxicity (relative to constant pH exposures) was observed when nymphs were exposed to extreme alkaline pH conditions for only 1 h/d in 96-h bioassays. The reduction of daily exposure periods to 1 h increased the calculated LC50 value 0.40–0.94 pH unit in laboratory and field tests, respectively, and the fiducial limits of the 1-h intermittent bioassays were significantly separated from the continuous-exposure LC50 values. These results indicated that 1-h daily exposures may enable insects such as *I. bicolor* to recuperate from alkaline pH to the extent that survival is enhanced.

Static and flow-through (artificial stream) tests conducted in the laboratory yielded equivalent results. The LC50 values for static and flow-through, constant-pH bioassays were 10.33 and 10.38, respectively (Table 1). For this reason, one can assume that bioassays conducted with *I. bicolor* in static test chambers are just as valid as those performed in artificial streams, since each apparatus evidently provided for the biological requirements of this test species.

Transmission Electron Microscopy

Reference *I. bicolor* coniform chloride cells (Fig. 1A) are characterized by a porous plate (P) and an associated plasma membrane (M) that possesses numerous infoldings that are thought to increase cytoplasmic surface area in the vicinity of ionic transport (Kapoor and Zachariah 1978). Cytoplasmic lamellae (L) extend into the basal portions of the cell complex where mitochondria are most dense.

Several distinct changes occurred in chloride cells ($n = 12$) exposed to sublethal levels of alkaline pH. After exposure to pH 10.0 for 96 h, vacuoles (V) appeared between the plasma membrane and porous plate (Fig. 1B), indicating the uptake and accumulation of water from the external medium. Cytoplasm in the apical region of the central cell became less dense and was displaced from the distal area to the central region of the gill.

Lethal levels of alkaline pH caused additional disruption of *I. bicolor* chloride cells. After 96 h at pH 11.0, vacuoles accounted for 30–80% of the volume of the cells (Fig. 1C), and the plasma membrane had withdrawn from an average of ~73% of the area of the porous plate in 19 cells examined. Membranous structures (M′), believed to include the displaced plasma membrane normally associated with the porous plate, were often left as remnants of the retracted cytoplasm. In areas where the cytoplasm had not completely withdrawn or been displaced to the basal portion of the gills, the cytoplasm was irregular and less dense than that of reference cells.

Experiments involving intermittent doses of alkaline pH showed similar results. At sublethal levels (i.e. pH 10.0), intermittent exposures consisting of 1 h/d at high alkaline pH and 23 h/d at ambient levels (~pH 8.0) over a 96-h period resulted in very slight morphological changes in chloride cell structure. Although the plasma membrane became separated from the porous plate and the cytoplasm became progressively less dense in some cells, 86% of the 14 cells examined appeared normal. Because these structural changes were minute, it is doubtful that they substantially altered the osmoregulatory capabilities of the nymphs.

Chloride cells intermittently exposed to pH 11.0 for 1 h/d over a 96-h period suffered drastic changes in ultrastructure. In every cell complex examined immediately after the last pH

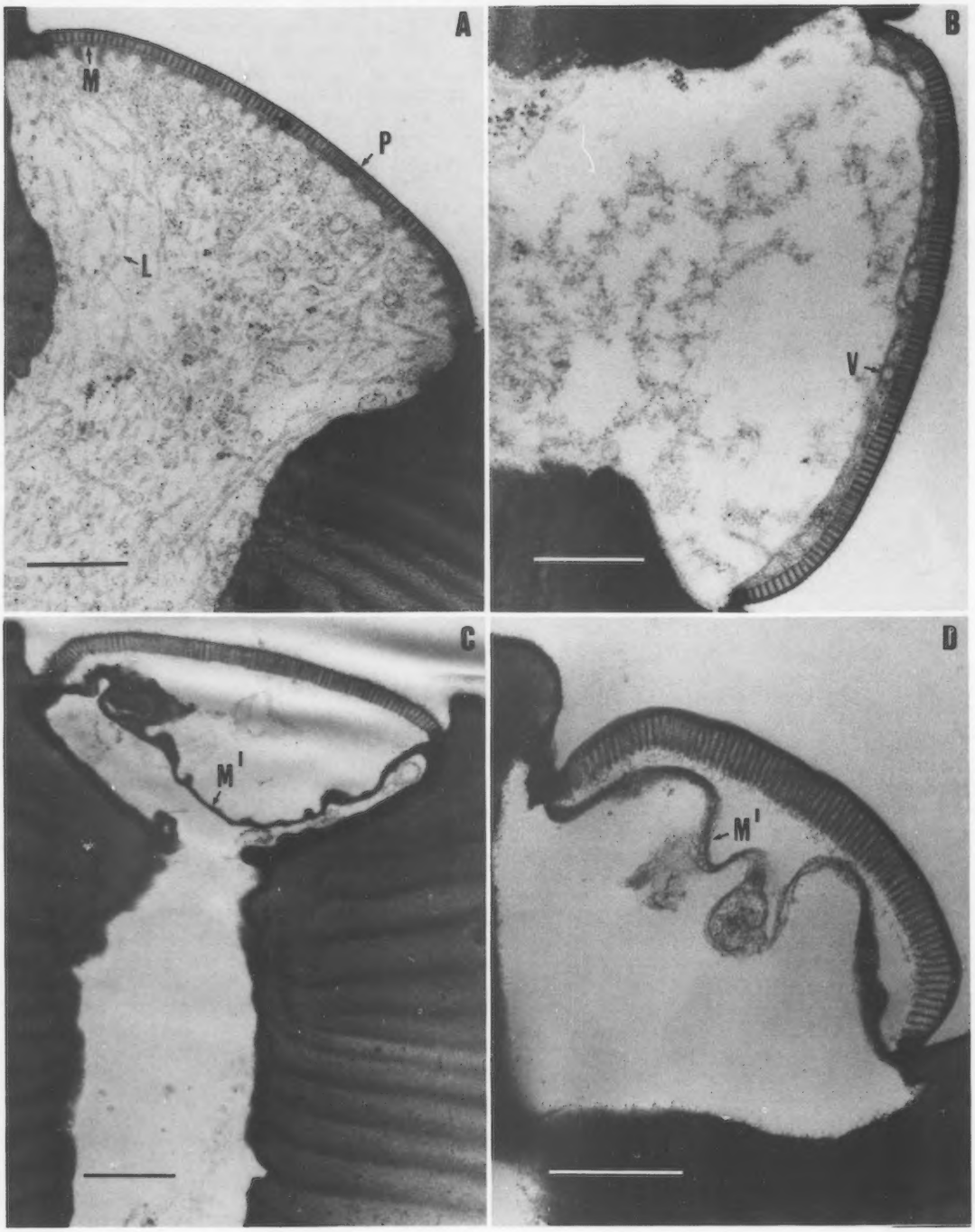

FIG. 1. Coniform chloride cells of *I. bicolor*. (A) Reference cell with plasma membrane (M), porous plate (P), and cytoplasmic lamellae (L); (B) cell continuously exposed to pH 10.0 for 96 h, exhibiting vacuole formation (V); (C) cell continuously exposed to pH 11.0 for 96 h, with membranous structures (M′) believed to represent the displaced plasma membrane; (D) cell exposed to pH 11.0 for 1 h/d for 96 h, also showing membranous structures. Horizontal bars in the lower left corner of each micrograph represent 1.0 μm.

exposure (n = 17), the cytoplasm was almost completely displaced or retracted from the apical portions of the cells, leaving fluid and small portions of cytoplasm near the porous plate (Fig. 1D). Macroscopic evaluations of *I. bicolor* supported these observations. All gills constantly or intermittently exposed to pH 11.0 for 96 h (n = 40) were distended due to the imbibition of water.

Nymphs intermittently exposed to lethal levels of alkaline pH were also evaluated for structural recovery through time. After 23 h of recovery from four daily 1-h exposures to pH 11.0, an average of 75% of the cytoplasm in the apical region of the chloride cells (n = 12) was restored to normal conditions of density and dispersion. By the eighth day following the exposure period, cytoplasmic lamellae, which interdigitate among the central cell and its adjacent cells, were reestablished, and these chloride cells could no longer be distinguished from reference cells. Such findings provide structural evidence that the coniform chloride cells of *I. bicolor* are able to recover from acute exposures to lethal levels of alkaline pH.

These TEM analyses confirmed hypotheses that alkaline pH disrupts chloride cell ultrastructure. Morphological changes, including the displacement of cytoplasm from the vicinity of the porous plate and the accumulation of fluids, were remarkably similar to those observed by Kapoor (1978) who studied the effects of different environmental salinities on the chloride cells of *Paragnetina media* (Plecoptera). In 75% of the chloride cells of nymphs held in distilled water, cytoplasm receded from the porous plate and large vacuoles appeared near the apex of the cell complexes (Kapoor 1978). Cells exposed to hypertonic solutions were also characterized by a degradation of the cytoplasm and vacuole formation, while those exposed to hypotonic solutions exhibited a proliferation of cellular membranes to increase surface area in the vicinity of the porous plate (Kapoor 1978). These changes took place in the chloride cells, while no corresponding changes occurred in the surrounding epidermal cells.

Although the observed ultrastructural changes in chloride cells exposed to alkaline pH were similar to those found in cells experiencing osmoregulatory stress in isotonic and hypotonic solutions, gills exposed to sublethal concentrations remained similar to reference tissues, with little or no noticeable fluid uptake. These findings indicate that extreme pH levels substantially impair the osmoregulatory capabilities of *I. bicolor*, while sublethal pH levels inflict no appreciable harm.

We propose that alkaline pH increased the number of Ca^{2+} and Mg^{2+} ions available for binding to openings in the porous plates, inhibiting the passive efflux of ions. Although pore size of mayfly coniform chloride cells (2.5 nm) is too great to regulate the passage of ions across the porous plate (Komnick and Stockem 1973), slight increases in Ca^{2+} and Mg^{2+} could substantially reduce pore size, decrease the normal rate of solute transfer, and cause osmoregulatory stress. The ensuing increase in chloride cell osmolarity resulted in an inward migration of water and distention of the cells.

Oxygen Consumption

Oxygen consumption results supported hypotheses that H^+ concentrations affect *I. bicolor* metabolic rate. Oxygen consumption at pH 10.0 (the LC10 value) and pH 11.0 was lower than that observed at pH 8.0 (Fig. 2). However, oxygen consumption at pH 11.0 was greater than that at pH 10.0, which indicated that sublethal pH levels caused a greater change in oxygen consumption (i.e. a greater decrease) than pH levels far above the LC50 value.

The magnitude of these differences in oxygen consumption (~24.2% difference between pH 8.0 and 10.0, ~13.1% difference between pH 8.0 and 11.0, and ~14.1% difference between pH 10.0 and 11.0 for a 10-mg insect using the log-transformed regression model) could not be evaluated statistically because the estimated regression lines were not parallel (Fig. 2). Using a non-log-transformed model that regresses oxygen consumption (microlitres per hour) with weight (milligrams), the regression lines diverge with increasing weight (Fig. 2, insert). Using log-transformed oxygen consumption and weight values, oxygen consumption was equivalent among larger insects exposed to pH 10.0 and 11.0, although these values were still below those associated with baseline respiration (pH 8.0). Despite the fact that these lines were not parallel, we feel that the differences in oxygen consumption are substantial and that they reflect an appreciable response due to alkaline pH exposure.

Although alkaline pH induced substantial changes in oxygen consumption, it is doubtful that this change in metabolic rate was caused by the energy requirements of maintaining ionic balances during osmoregulatory stress. Kapoor (1979) found that extreme variations in environmental salinity caused no corresponding changes in oxygen consumption and concluded that the metabolic costs of osmoregulation were extremely small and almost undetectable. Assuming the metabolic costs of osmoregulation were manifested in oxygen consumption, energy utilization in response to osmoregulatory stress would be expected to cause an increase in oxygen consumption, rather than the decrease observed in *I. bicolor*. For this reason, we believe that oxygen consumption was hindered during alkaline pH stress by the accumulation of fluids in the gill tissues documented in the electron microscope analysis.

In conclusion, alkaline pH caused osmoregulatory stress at elevated pH by inhibiting the passive efflux of ions from the coniform chloride cells of the gills. Ensuing increases in gill osmotic pressure resulted in an accumulation of fluids that disrupted the transfer of respiratory gases and decreased oxygen consumption. Consequently, respiratory difficulty and osmoregulatory stress were thought to account for the mortality observed in *I. bicolor*.

Isonychia bicolor is highly sensitive to both constant and intermittent doses of alkaline pH exceeding pH 11.0. Although intermittent exposures substantially reduce mortality, osmoregulatory difficulty and respiratory stress still cause appreciable harm whenever these insects are exposed to pH levels $\geq$11.0. Despite this sensitivity, major structural recovery was evident within 4–8 d in chloride cells of *Isonychia* damaged by exposures of 1 h/d to pH 11.0 (for 96 h). The damaging effects of alkaline pH were not observed in oxygen consumption experiments and TEM analyses conducted at any level below pH 10.0. Since intermittent (1 h/d) 96-h LC50 values were $\geq$10.48 in both laboratory and field tests, accidental discharges of alkaline effluents lasting up to 1 h in the pH 9.0–10.0 range are not thought to be acutely hazardous. Consequently, the pH 9.0 limit imposed by regulatory agencies may require site-specific revision to a level of pH 9.5 depending upon abiotic and biotic parameters in the receiving system. Decisions to conduct site-specific analyses in preparation for applications concerning such variances should be based upon chemical analyses of

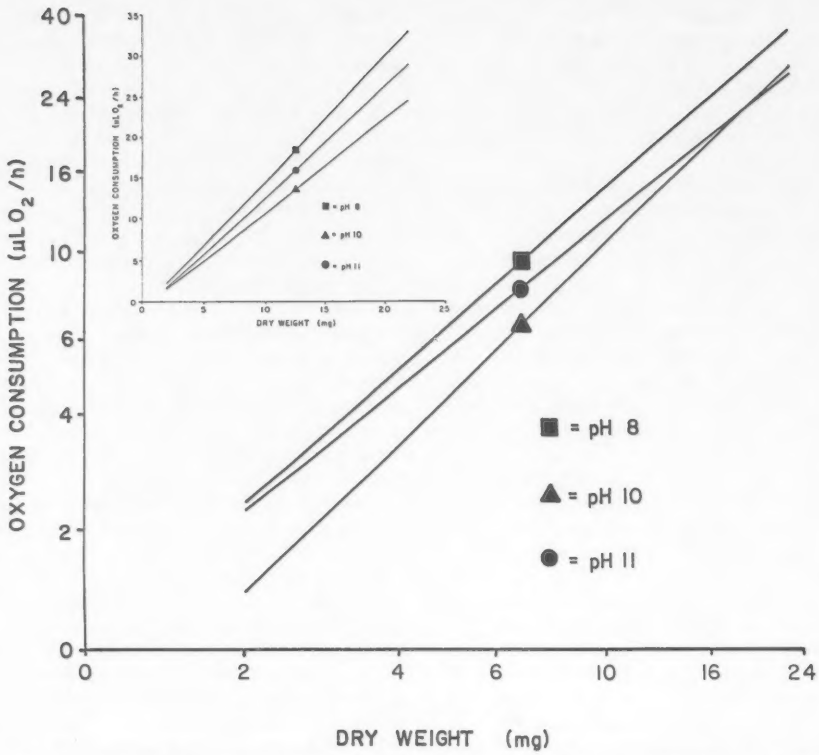

FIG. 2. Estimated regression lines for *I. bicolor* oxygen consumption (log-transformed data) for pH 8.0 ($R = 0.025 + 1.113W$, $R^2 = 0.857$, $n = 77$), pH 10.0 ($R = -0.268 + 1.286W$, $R^2 = 0.798$, $n = 69$), and pH 11.0 ($R = 0.037 + 1.037W$, $R^2 = 0.852$, $n = 77$). Inset illustrates alternate interpretation of oxygen consumption values that arises when data are not log-transformed (pH 8.0, $R = -1.223 + 1.555W$, $R^2 = 0.842$, $n = 77$; pH 10.0, $R = -0.972 + 1.166W$, $R^2 = 0.873$, $n = 69$; pH 11.0, $R = -1.244 + 1.369W$, $R^2 = 0.874$, $n = 77$).

stream and effluent water quality (e.g. buffering capacity, Ca^{2+} and Mg^{2+} levels, and dilution capability), the responses of sensitive insect species, and the ability of the industry to control the release of alkaline effluents. Substantial reductions in the cost of effluent acidification may be realized if similar analyses of gill ultrastructure obtained in this study fail to document appreciable harm to sensitive species, such as *Isonychia*, that inhabit the receiving system when daily, intermittent releases up to pH 9.5 occur.

Acknowledgments

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Relationship of Crayfish (*Orconectes virilis*) Growth to Population Abundance and System Productivity in Small Oligotrophic Lakes in the Experimental Lakes Area, Northwestern Ontario

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Crayfish growth in four lakes in the Experimental Lakes Area (ELA) was examined by analysis of size–frequency distributions, molt increment data, and calculation of instantaneous growth and mean size at onset of sexual maturity. *Orconectes virilis* growth rates at ELA are only 27–38% of those reported for other areas. Growth varied both among study lakes and between years. Higher temperatures and a longer growing season during 1980 increased growth an average of 12% over that of the preceding year. Crayfish growth and maximum size in four to six lakes were significantly correlated with phytoplankton production and chlorophyll *a* concentration. Growth regulated both the number of age I animals attaining sexual maturity and the per capita egg production, and was also directly related to the proportion of mature females that were fertilized. I believe population regulation is mediated through alterations in reproductive capacity that is correlated with system productivity.

Les distributions des fréquences de longueurs, les données sur l'accroissement à chaque mue et les calculs du taux instantané de croissance et de la taille moyenne au début de la maturité sexuelle ont servi à l'analyse de la croissance de l'écrevisse dans quatre lacs de la zone des lacs expérimentaux (ZLA). Dans celle-ci, les taux de croissance de *Orconectes virilis* ne s'élèvent qu'à 17–38 % de ceux qui sont signalés à d'autres endroits. La croissance variait d'un lac expérimental et d'une année à l'autre. En 1980, des températures plus élevées et une plus longue saison de croissance ont entraîné un accroissement de 12 % du taux de croissance par rapport à l'année précédente. Le taux de croissance et la taille maximum des écrevisses dans quatre des six lacs étaient en corrélation significative avec la production phytoplanctonique et la concentration de chlorophylle *a*. Le taux de croissance régissait le nombre d'animaux âgés de 1 an qui avaient atteint la maturité sexuelle et la production d'œufs par individu; ce taux était aussi en rapport direct avec la proportion de femelles matures fertilisées. Selon l'auteur, le contrôle démographique est modulé par des modifications de la capacité de reproduction en corrélation avec la productivité d'un système.

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Empirical limnology has received considerable attention in recent years as a predictive tool in addition to serving as a unifying force between different paradigms (Rigler 1982). Attempts must now be made toward replacing these empirical theories with explanatory ones to increase our understanding of both trophodynamic ecology as well as yield variability (Kerr 1982; Rigler 1982). The causes of events are ultimately more important than the events themselves, as Cicero has said. Although numerous aquatic studies have empirically linked consumers to some measure of phytoplankton abundance, rarely have these relationships been explained on the basis of life history variables — growth, mortality, or reproductive capacity — known to influence population dynamics and production (Nakashima and Leggett 1975; Dermott et al. 1977; Mills 1985). In a recent review, Momot (1984) speculated that nutrient availability, by governing the nature of food production, can directly influence the demographic response and production of crayfish at various latitudes. Nakashima and Leggett (1975) cited several reports showing that in food-limited oligotrophic systems, fish productivity can be determined by changes in organism growth.

The purpose of this study was to determine the natural variability of *Orconectes virilis* (Hagen) growth among four basins in the Experimental Lakes Area (ELA), northwestern Ontario, as influenced by system productivity, and to ascertain the relationship of growth rate to population abundance within these study lakes. Newman and Pollock (1974) found that lobster growth within localized regions of similar thermal regime depended upon the benthic biomass available as food, which in turn was correlated with primary productivity. Capelli (1975) concluded that although substrate suitability probably determined some upper limit for size of a potential crayfish population in a given lake, some other unmeasured factor(s) determined to what extent that potential was realized. In regions containing oligotrophic lakes such as those in ELA, where

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crayfish growth is extremely restrained and sexual maturity closely associated with body size, I suggest that small differences in growth will exert substantial influences upon reproductive capacity and the rate of population increase.

Description of the Study Lakes

ELA is situated at 93°30′, 94°00′W and 49°30′, 49°45′N, 300 km east of Winnipeg, Manitoba. ELA is a headwater region containing small glacially formed basins in the Precambrian Shield. Lakes are oligotrophic, ice-covered during November through May and have dimictic thermal regions. *Orconectes virilis* is the only crayfish species present in these lakes. Four ELA lakes were selected for detailed field study of crayfish life history in 1979 and 1980: Lake 223 (L223), L224, L239, and L240. Lake 223 has been undergoing experimental acidification with sulfuric acid since 1976 (Schindler et al. 1980). At the time of this study, growth of *O. virilis* had not been affected by lake acidification to pH 5.4–5.6 (France 1983). The other three lakes are circumneutral and considered reference lakes for the region. Physical and chemical data for these lakes are available in Brunskill and Schindler (1971), Hesslein et al. (1980), and Prokopowich (1979). The extent of shoreline formations (beaches, boulders, swamps, cliffs) is similar for all lakes, and annual thermal cycles are nearly identical. Light attenuation, chlorophyll *a* concentration, and areal phytoplankton production increase from L224 to L223/L240 to L239 (Prokopowich 1979; Fee 1980).

Oronectes virilis is a non-burrowing crayfish species with a characteristic habitat preference for rocky bottomed lakes and streams within the Canadian Shield (Crocker and Barr 1968). Morphometric surveys of ELA lakes showed that 70–80% of the littoral zone extending to a depth of about 5 m and representing 15–17% of the total lake surface area is composed of broken rock shelf and large boulders (50–100 cm in diameter) (Stockner and Armstrong 1971). The suitability of littoral habitats as nursery areas affecting recruitment of young (Momot and Gowing 1983) was similar in all four lakes. Because of the small size of the study lakes (25.9–56.1 ha), and knowledge that crayfish are capable of extensive movement (Capelli 1975; Flint 1977), I believe that discrete subpopulations of *O. virilis* do not exist within individual ELA lakes. Flint and Goldman (1977) found that crayfish growth can be strongly influenced by differences in quantity and mean size of stones. Extreme care, therefore, was taken to ensure that the collection sites chosen among the study lakes were of uniform physical characteristics. The geomorphology of these collection sites corresponded to Capelli's (1975) "type-A substrate" (mostly rocks and gravel, high shelter potential) found to be most suitable for crayfish growth and abundance. At least three different sampling areas were chosen within each lake. Their precise locations are detailed in France (1983).

Materials and Methods

Methods of Collection

Crayfish were collected with SCUBA to obtain a representative sample of the population (Capelli 1975). Problems involved with capture of ovigerous females from between boulders and elusive young, directly by hand collection, were alleviated with the aid of a diver-operated suction gun which proved over 90% effective in capture of all crayfish, irrespective of size or sex, that were seen. Exposed animals were collected at night over the depth range 0–6 m. In 1979 and 1980, all four populations were sampled once during the spring (late May – early June) before onset of the first molting of mature males or hatching of eggs from ovigerous females, and once again in the autumn (mid-September – mid-October) following completion of the last molt of juveniles and mature males. Additional midsummer collections were made twice in L223 and once in L239 during 1979, and once in both L223 and L240 during 1980. Between 193 and 294 crayfish were collected for every sampling period. Rostrum carapace length, usually about half total length (France 1983), weight, sex characteristics (pleopod I or II in males, presence of eggs or cement gland development in females), and molting stage assessment were recorded from specimens.

To relate crayfish growth rate to population size, I obtained two independent estimates of relative abundance from the study lakes. In 1979, the mean catch per hour of SCUBA search time was calculated from five dives within each lake during autumn. In mid-July 1980, when the majority of the crayfish were in the intermolt condition and most active because of high water temperatures, 20 modified minnow traps baited with macerated fish were set throughout the SCUBA collection areas. To eliminate catch bias due to size and sex dominance (Brown and Brewis 1978), only the number of adult males caught per trap was compared. Capelli (1975) showed that catches of adult males were strongly correlated with diver-determined densities and could be used as an index of relative crayfish abundance between lakes. Yellow perch (*Perca flavescens*) sizes and densities are believed to be too small (K. Mills, Freshwater Institute, Winnipeg, Man.) to substantially influence midsummer trapability, as in Collins et al. (1983).

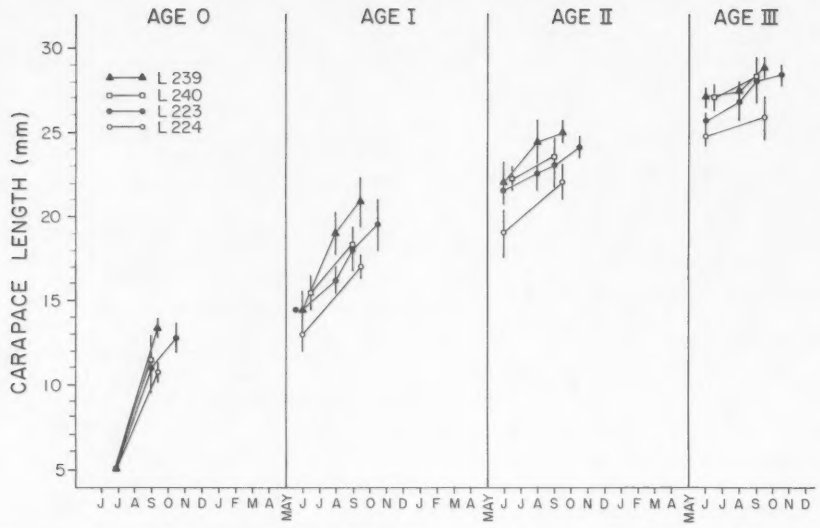
Crayfish were also sampled from several other lakes of increasing mesotrophy within or near ELA to increase the sample size for regressions between crayfish growth and primary production as measured by chlorophyll *a* concentration (Fee 1979). The mean size of the 15 largest crayfish collected during August 1980, representing age IV males just before their mortality, was used for an index of growth rate (Momot et al. 1978), as extensive seasonal collections needed for calculation of the latter were not possible. Collection sample sizes were 1505 from L223, 921 from L224, 1083 from L239, 1328 from L240, 108 from L302S, and 129 from Roddy Lake for ELA basins and 87 from Kenora Harbour (Lake-of-the-Woods), 173 from Clay Lake, and 92 from Falcon Lake for nearby non-ELA basins.

Growth Analysis

Growth of age classes was assessed by analysis of population length–frequency distributions (France 1983), which for this species produces an accuracy of 80% for correct ageing (Momot 1967). Cumulative frequencies were plotted on probability paper to enhance the discrimination of size data into discrete components (Cassie 1954) permitting the assignment of mean size values and corresponding standard deviations to each age class (Momot 1978; Jones 1981). Data for both sexes were combined as in Hopkins (1966) because preliminary separation of sexes demonstrated the same pattern as the conjoined results.

Data on growth increment per molt were obtained by collecting animals nearing ecdysis from one lake (L240) and retaining them in laboratory aquaria. Only results from those crayfish that molted within 5 d were used. The number of molts completed by young-of-the-year (age 0) crayfish was calculated using the formula of Van Deventer (1937):

$$Z = (x - y/\text{increment}) + 2$$


AGE 0
AGE I
AGE II
AGE III
L 239
L 240
L 223
L 224
CARAPACE LENGTH (mm)
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25
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15
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FIG. 1. Growth of *O. virilis* in ELA. Symbols indicate mean sizes ± SD from the probit plot method of Cassie (1954) for crayfish collected during 1979. Sample sizes were between 193 and 294 for all collections.

where Z represents the number of immature molts, x and y are means of the size group at the beginning and end of the season, and the value 2 denotes the number of molts while still attached to the maternal female.

Values of mean carapace length at the beginning and end of the growing season (late May – mid-September) before and after the appropriate molting periods, and corresponding to the average number of days with water temperatures above 10°C (155 d, see Discussion), were obtained from the growth diagram. These were then converted to weight units by the length–weight relationships determined for each lake (France 1983). The instantaneous growth rate (G) was calculated for all age groups within each lake after Ricker (1975):

$$G = \log_e (W_t/W_0)$$

where G is the instantaneous growth rate (grams per unit of time), W_0 is the initial weight (grams), and W_t is the final weight after 155 d. Growth was also expressed as the relative percentage increase in size (R) such that

$$R = (l_2 - l_1)/l_1 \times 100$$

where l_1 is the initial carapace length (millimetres) and l_2 is the final carapace length at the end of the growing season (Ricker 1975).

To confirm growth rate differences among the four *O. virilis* populations, I plotted cumulative percent of mature females and form I males against carapace length on probability paper to calculate the mean size at onset of sexual maturity (Wenner et al. 1974). Mature females represent ovigerous animals plus unfertilized individuals with obvious cement glands and in the process of resorbing ovarian eggs.

Results

Crayfish in L239 were the largest in mean size for every age class, while those in L224 were invariably the smallest (Fig. 1). Mean carapace lengths for L240 and L223 crayfish were intermediate and similar. No increase in size occurred during the 6-mo winter period.

The mean percentage growth increment per molt decreased with age: 14.8% for age 0 crayfish ($n = 11$), 11.0% for age I ($n = 5$), 6.6% for age II ($n = 18$), and 2.6% for age III ($n = 5$). The average growth increment per molt for L240 crayfish was calculated as 1.5 mm for age 0, 1.7 mm for age I and II animals, and 1.4 mm for age III class by using the relationship postmolt C.L. = 2.37 + 0.97 premolt C.L., $r = 0.99$, $n = 39$, and the mean sizes obtained from Fig. 1 for the correct time of molting. Age 0 *O. virilis* completed seven molts during their first growing season. Immature age I crayfish molted three or four times, and mature age II and III males molted twice and females only once.

Annual growth rates declined with age in all lakes (Table 1). L224 crayfish had the slowest rate of growth and L239 crayfish the highest. Growth in 1980 exceeded that in 1979 by an average of 12%. Between-year differences in growth ranged from 8% in L239 to 15% in L224.

The percentage of mature crayfish within a particular size class varied among the lakes (France 1983). Mean sizes at onset of sexual maturity correlated with observed growth rate differences both between different lakes and years (Table 2); e.g. growth retardation in L224 and during 1979 for all populations was expressed by reduced maturity size indices.

The mean sizes of crayfish were related to average annual primary production in ELA study lakes ($r = 0.85$, 0.95, 0.94, and 0.99 for age groups 0–III, respectively). As expected, correlations were highest for age III crayfish whose present size reflects the cumulative effects of 4 yr of growth. Sizes of young-of-the-year would be more closely correlated to primary production during that particular year rather than a 4-yr averaged value. The average rate of growth was also related to the phytoplankton production ($r = 0.84$). Unfortunately, due to the small sample size ($n = 4$), only the relationship of age III

TABLE 1. Growth rates of *O. virilis* at ELA calculated over 155 d during summer 1979 and 1980. Sample sizes were 413 and 366 in L224, 965 and 578 in L223, 495 and 573 in L240, and 640 and 349 in L239 for 1979 and 1980 calculations, respectively. G = instantaneous growth rate ($\log_e W_2 - \log_e W_1$); R = relative % growth rate ($(l_2 - l_1)/l_1 \times 100$).

		L224		L223		L240		L239		Average	
Year	Age	*G*	*R*	*G*	*R*	*G*	*R*	*G*	*R*	*G*	*R*
1979	0	1.16	144.4	1.34	157.8	1.29	173.3	1.47	197.8	1.32	168.3
	I	0.27	23.1	0.34	27.6	0.32	24.3	0.49	44.1	0.36	29.8
	II	0.19	10.5	0.11	8.4	0.11	9.2	0.17	13.6	0.15	10.4
	III	0.05	3.6	0.13	9.7	0.07	6.0	0.08	7.0	0.08	6.6
	Total	1.67	181.6	1.92	203.6	1.80	212.8	2.20	262.4	1.92	215.1
1980	0	1.22	155.5	1.39	166.7	1.37	184.4	1.53	211.1	1.38	179.4
	I	0.37	28.0	0.43	35.7	0.28	23.3	0.36	29.7	0.36	29.2
	II	0.18	15.3	0.22	17.1	0.21	16.7	0.32	25.7	0.23	18.7
	III	0.11	10.9	0.16	11.8	0.16	12.2	0.18	14.5	0.15	12.4
	Total	1.88	209.7	2.20	231.3	2.02	236.6	2.39	281.0	2.12	239.7

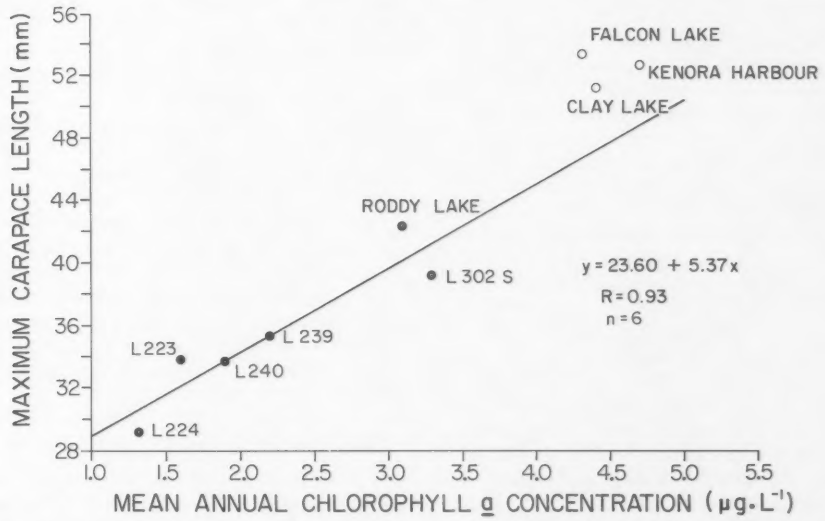

FIG. 2. Relationship of mean maximum *O. virilis* size (described in text) to epilimnion chlorophyll *a* concentration in six ELA lakes. Data for non-ELA lakes: Kenora Harbour (Lake-of-the-Woods), Falcon Lake, and Clay Lake (open circles) were not included in the calculation. Chlorophyll data for ELA from Fee (1979, 1980) and for other nearby Canadian Shield lakes from J. Donnets, Ontario Ministry Natural Resources, Kenora, Ont. (pers. comm.), Manitoba Department of Mines and Resources, and J. Rudd, Freshwater Institute, Winnipeg, Man. (pers. comm.).

TABLE 2. Mean carapace length (mm) at onset of sexual maturity for ELA *O. virilis* as calculated by the probit plot method of Wenner et al. (1974). Sample sizes were between 72 and 131, and standard error about the mean averaged ±0.22 mm. Values represent males collected during the autumn of the year listed and females sampled the following spring.

	1978		1979		1980	
Lake	M	F	M	F	M	F
L239	—	22.0	22.6	21.6	23.6	—
L240	—	21.4	22.2	20.8	23.1	21.3
L223	22.4	20.1	22.2	19.8	22.8	20.7
L224	—	19.2	21.5	—	22.0	—

mean size to algal production was significant at the $p = 0.05$ level. Extending the sample to other nearby lakes, the relationship to chlorophyll *a* concentration explained 87% of the variation in maximum crayfish size among six ELA lakes (Fig. 2). Non-ELA lakes were not included in the regression for reasons outlined in the discussion.

The growth rate of crayfish in ELA lakes was positively related to the percentage of age I animals that attained sexual maturity before winter, and was inversely related to the percentage of mature females that remained unfertilized by the following spring (Table 3). Due to correlations between size of maternal female and number of eggs (R. L. France, unpubl. data), there was a direct relationship between growth rate and egg production in these lakes. Crayfish growth was ultimately directly correlated with relative population abundance.

TABLE 3. Relationship of *O. virilis* growth to reproduction and population abundance in the ELA region.

Lake	Relative % growth increase	% age I sexually mature (n)	% mature females unfertilized	Mean ovarian egg count (n)	Relative abundance (catch per hour of effort) ±SE	Number adult males/trap	Number[a] crayfish/m^2
L239	262.4	F 80 M 65 73 (123)	3.3	98.1 (55)	65±6	5.5	1.97
L240	212.8	F 70 M 50 60 (82)	9.1	88.3 (49)	51±4	3.3	1.19
L223	203.6	F 65 M 35 50 (151)	11.5	88.7 (43)	53±6	3.3	1.17
L224	181.6	F 10 M 0 5 (110)	18.8	77.7 (31)	33±5	1.7	0.59

[a]Calculated from modified fig. 9 in Capelli (1975); number/m^2 = −0.01 + 0.36 (number adult males/trap), $r = 0.95$, $n = 5$.

Discussion

Growth Variation

Orconectes virilis from ELA exhibit the smallest sizes recorded for this species at any location (France 1983). I consider three factors to be of importance in limiting crayfish growth in the present group of Precambrian Shield lakes.

Molting in *O. virilis* ceases when water temperatures decline below 10°C (Aiken 1967), so no overwinter growth occurs. Spring molting in ELA lakes was delayed compared with *O. virilis* populations elsewhere. This short and cool growing season will tend to restrict crayfish growth in northern populations (Momot et al. 1978). The 1979, spring was one of the coldest on ELA record with ice-out not occurring until May 13, compared with the exceptionally hot spring of 1980 with ice-out on April 25. In 1979 the growing season (above 10°C) was 140 d, while crayfish in 1980 had 164 growing days (K. Beaty, Freshwater Institute, Winnipeg, Man., unpubl. data). The growing season in 1978, a more typical ELA year, was 155 d. The average 12% increase in rate of growth during 1980 over that of the preceding year can, in part, be attributed to the two extremes in average spring temperatures and the resulting 2-wk advancement of molting events.

Crayfish growth at ELA is strongly food limited so that even lakes with similar temperatures within a small area can display wide differences in growth. The large sizes obtained by *O. virilis* in Roddy Lake and nutrient-rich Kenora Harbour, Falcon Lake, and Clay Lake are comparable or slightly larger than values tabulated by Momot et al. (1978) for more southerly populations. The seasonal differences in growth rate between the two extreme temperature years (about 12%) are much less than growth variations among lakes (about 30% between L224 and L239 populations). The relationship between *O. virilis* growth and trophic status of ELA lakes, as measured by phytoplankton production or chlorophyll *a* concentration, is attributable to food intake. Although suspended algae may be utilized by crayfish (Budd et al. 1979), analysis of stomach contents indicates *O. virilis* at ELA rely more heavily upon other food sources such as autochthonous organic matter, chironomids, and epilithic periphyton, all of which increase in proportion with phytoplankton production in ELA lakes (Prokopowich 1979; Davies 1980; Stockner and Armstrong 1971; Schindler et al. 1973). The importance of phytoplankton production as a quantitative indicator of crayfish diet at ELA is also shown by the demonstration that it may explain, in part, the seasonal differences observed in crayfish growth. The order of increasing yearly variability in epilimnetic production from L239 to L223 to L240 to L224, depending on lake residence times (Fee 1980), corresponds to the increasing magnitude of variation in annual growth of *O. virilis* in the four study lakes.

Orconectes virilis inhabiting oligotrophic ELA lakes with limited macrophytes heavily consume allochthonous plant detritus from the surrounding watersheds. The restricted growth of ELA crayfish compared with those elsewhere is partially explained by the higher predominance of marginally suitable coniferous detritus (Momot et al. 1978) within these lakes (Jones and Momot 1981; Brunskill and Schindler 1971). Further, the greater size per unit of chlorophyll concentration of crayfish from the three non-ELA lakes compared with those predicted from the restricted data set of ELA lakes (Fig. 2) is in accordance with the greater relative proportion of deciduous vegetation within their watersheds (Falcon Lake, especially, is located just on the edge of the Canadian Shield near the Manitoba–Ontario border).

Relationship of Growth to Population Control

Previous studies with crayfish have dealt with populations of high density (up to $27.5 \cdot m^{-2}$) and not surprisingly have found inverse relationships between density and growth due to competitive food shortages (Hopkins 1966; Abrahamsson 1966; Morrissy 1975). Much more common, however, are populations so strongly influenced by extrinsic factors such as relative shortage of suitable food (White 1978) that rarely do they reach sizes where density-dependent factors become important (Poole 1974). Crayfish lipid reserves can decrease dramatically during midsummer, indicating that food is severely limiting in such situations (Armitage et al. 1972). In these cases, as White (1978) demonstrated, food resources can be so scarce in the environment as to be limiting regardless of competitive pressures. In ELA, where growth has been shown to be food-limited, and crayfish densities are among the lowest reported in the literature ($0.59–1.97 \cdot m^{-2}$), individual growth controls, rather than is controlled by, population growth rate. This control is mediated through alterations in reproductive capacity.

As a result of greatly reduced growth, only 5% of L224 crayfish exceed the size boundary of sexual maturity (approximately 20 mm C.L.) during their second season of growth (Fig. 1) compared with nearly three-quarters of the age I L239 population (Table 3). The majority of recruitment into the L224 population therefore occurs through reproduction of the age II

class after an additional year of growth. Due to high mortality rates (France and Graham 1985), the age II class is numerically only one-third to one-half that of the age I size class. The effective breeding population in L224 is much smaller than those present in L223 and L240, which in turn are less than that in L239. Cole (1954) and Lewontin (1965) showed that the age at first reproduction, particularly within short-lived species (such as crayfish), was the single most important factor affecting rate of population increase.

Crayfish secrete no known sexual pheromone (Mason 1970), and mating is dependent upon the random meeting of mature animals (Weagle and Ozburn 1972). Pairings may be restricted in northern populations such as those at ELA with long winters of low temperature due to decreased crayfish movement (Capelli 1975; Flint 1977). Capelli (1975) hypothesized that in sparser crayfish populations, the distance between individuals might severely limit the frequency of contact during the winter, producing a greater chance that a female had not mated at any given time (the "Allee-effect") (Odum 1975). At ELA the size of breeding populations directly determined the percentage of copulatory pairings among mature adults (Table 3). Because of the dependence of egg counts on size of maternal female, populations with faster growing individuals will proportionally produce a larger recruitment of young. These results combine to indicate a direct relationship between crayfish growth and rate of population increase in ELA lakes.

However, my observations over 3 yr in the study lakes, and detailed measurements over 6 yr by I. J. Davies (Freshwater Institute, Winnipeg, Man., unpubl. data) of annual density variation in L223, indicate that population stability is characteristic of crayfish inhabiting ELA lakes. Although L239 starts out with many more individuals each year, a higher percentage of its population potentially reproductive, and a higher per capita egg production than any of the other three lakes, its population still does not greatly vary from year to year. This implies that L239 is capable of maintaining a certain number of crayfish, its equilibrium density (Nicholson 1954), by some balancing mechanism in relation to the level of adequacy of the environment, probably determined by the relative shortage of food resources (White 1978). Because L224 has a much lower productivity, it can support fewer crayfish. Two factors, food-controlled recruitment and density-dependent mortality, are known to strongly regulate brood size of crayfish populations and narrow the resulting survivors at maturity to within a very restricted range of density (Momot 1984).

White (1978) cited numerous examples of how shortage of food detrimentally affects survival in the first year of life. In particular, Momot (1984) showed that life cycles of crayfish are adjusted to food availability. This results in a matching of young-of-the-year production to the food production of each habitat. Crayfish populations are also regulated by intrinsic feedback loops on recruitment and survival of young (Morrissy 1975; Momot and Gowing 1977). This age-specific mortality is particularly effective in reducing fluctuations in density within crayfish populations inhabiting low-energy, low-nutrient environments such as those at ELA (Momot 1984). Additionally, L239 and L240 contain abundant populations of several species of predaceous fish which preferentially prey upon age 0 crayfish (Stein 1977; Gowing and Momot 1979) and are absent from the less productive lakes, L223 and L224. Together, I believe these factors maintain a degree of population homeostasis for *O. virilis* at ELA by providing a higher per capita mortality rate among the potentially faster growing populations.

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Chemistry of Lake Hovvatn, Norway, Following Liming and Reacidification

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Wright, R. F. 1985. Chemistry of Lake Hovvatn, Norway, following liming and reacidification. Can. J. Fish. Aquat. Sci. 42: 1103–1113.

Hovvatn, a 1-km^2, chronically acidified lake in southernmost Norway, was treated with 200 metric tons of powdered limestone in March 1981. An additional 40 metric tons was added to a 0.046-km^2 pond (Pollen) draining into Hovvatn. At ice-out, pH rose from 4.4 to 6.3 (Hovvatn) and 7.5 (Pollen), Ca and alkalinity increased, and total Al decreased by about 120 μg/L. The amount of limestone dissolved, calculated from the lake Ca budgets, was 50% after 3.5 yr in Hovvatn and 25% in Pollen. A greater fraction dissolved at Hovvatn because the limestone lay in the active surf zone. In Pollen, limestone that was not dissolved at ice-out formed a layer on the sediment surface from which only minimal dissolution occurred. Hovvatn and Pollen reacidified to pH 4.9 and 5.5, respectively, 3 yr after liming. A simple flushing model describes the reacidification of Pollen. In Hovvatn, however, dissolution of additional limestone during the 3.5 yr since liming has considerably slowed reacidification.

Le lac Hovvatn, un lac chroniquement acide (1 km^2) situé dans la partie la plus au sud de la Norvège, a été traité avec 200 t de calcaire en poudre en mars 1981. De plus, 40 t ont été ajoutées à l'étang Pollen (0,046 km^2) qui se déverse dans le lac Hovvatn. À la débâcle, le pH est passé de 4,4 à 6,3 (Hovvatn) et à 7,5 (Pollen) tandis que l'alcalinité et le Ca augmentaient; l'Al total a baissé d'environ 120 μg/L. La quantité de calcaire dissoute, calculée à partir des bilans lacustres en Ca, s'élevait à 50 % dans le lac Hovvatn et à 25 % dans l'étang Pollen après 3,5 années. Dans le premier, une plus grande quantité s'est dissoute parce que le calcaire était présent dans la zone active de ressac. Dans le second, le calcaire non dissous au moment de la débâcle a formé une couche sur le sédiment superficiel d'où seule une faible dissolution a eu lieu. Trois ans après le chaulage, le lac Hovvatn et l'étang Pollen étaient redevenus acides : dans le premier, le pH atteignait 4,9 et dans le second, 5,5. Un simple modèle de renouvellement des eaux décrit la réacidification de l'étang Pollen. Toutefois, la mise en solution de calcaire supplémentaire au cours des 3,5 années depuis le chaulage a considérablement ralenti la réacidification du lac Hovvatn.

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Acid precipitation, acidification of freshwaters, and loss of fish populations has affected thousands of lakes and streams in southern Norway (Jensen and Snekvik 1972; Overrein et al. 1980). Years before the cause of the acidic surface waters was known, Atkin (1922) discovered that neutralization with materials such as limestone or marine shell sand reduced the toxicity to salmonid fish. As early as in the 1920s, acidic waters were treated in fish hatcheries in southern Norway (Sunde 1926). In several cases local fisheries clubs successfully limed small lakes for put-and-take brown trout (*Salmo trutta*) fishing.

In 1980 the Norwegian government started a 5-yr research project with the goal of documenting to what extent neutralization (liming) provides a feasible biological, technical, and economic means of reducing the damage caused by acidification (Matzow 1982). Hovvatn, a chronically acidic lake in southernmost Norway, was chosen as one of the sites to be studied as part of the Norwegian liming project. The objectives were to compare two liming techniques and to document changes in the lake system following liming and subsequent reacidification. I report here the changes in water chemistry at Hovvatn before and during a 3.5-yr period following liming. I have previously described the first (Wright 1982), second (Wright 1984a), and third year's results (Wright 1984b).

Study Area and Liming

Hovvatn is a 1.1-km^2 lake with a 5.8-km^2 terrestrial catchment, 500 m above sea level, 50 km north of Kristiansand (Fig. 1). The catchment is of granitic bedrock with thin to nonexistent, poorly developed podzolic and mor soils. Open forest of spruce (*Picca abies*), pine (*Pinus sylvestris*), and birch (*Betula verrucosa*) are interspersed with peaty areas. Hovvatn has a mean water residence time of about 0.8 yr (Table 1). Shore morphology is complicated with numerous bays and islands (Fig. 1). A small 4.6-ha pond (called Pollen) is attached to the eastern arm of the lake by a 1-m-wide shallow channel. The liming experiment at Hovvatn comprised two parts: liming of Hovvatn itself and liming of Pollen. Lille Hovvatn, a small lake draining into Hovvatn from the south, was used as the untreated control.

Hovvatn is a privately owned lake. Journal records kept by the local fishermen indicate that Hovvatn supported brown trout until 1948. A scientist from the Norwegian Directorate for

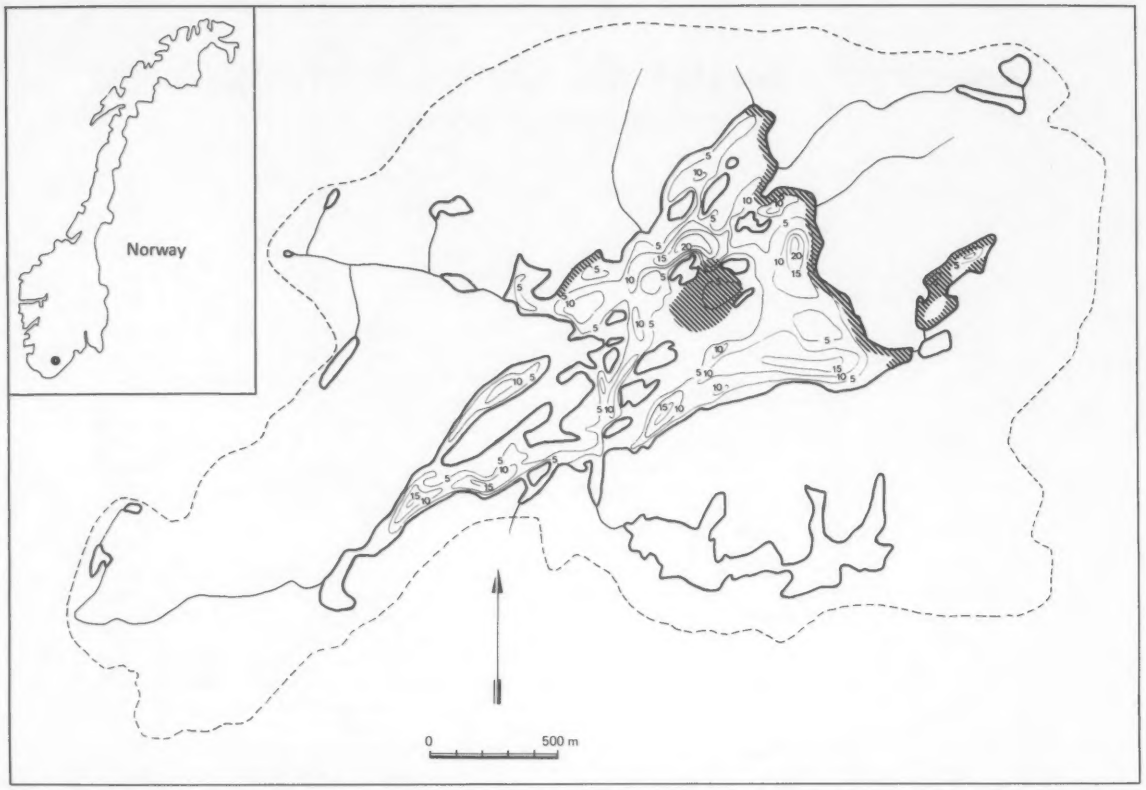

FIG. 1. Study lake Hovvatn and its catchment showing location of the pond Pollen (at east end) and the control lake Lille Hovvatn (south of Hovvatn). Hatched areas received limestone.

TABLE 1. Morphological and hydrological characteristics of Hovvatn and Pollen.

Lake area (km^2)	1.14	0.046
Catchment area including lake (km^2)	6.96	0.30
Average depth (m)	5.6	3.3
Maximum depth (m)	22.0	10.0
Volume (10^6 m^3)	6.4	0.15
Hydraulic retention time (yr)[a]	0.8	0.4

[a]Lake volume/annual outlet discharge assuming discharge of 1250 mm/yr.

Game and Freshwater Fish (DVF) visited Hovvatn in the 1930s and reported that trout spawned in shallow, sandy areas between the islands. In spite of repeated stockings in the 1950s, no fish have been caught since 1948. Test fishing conducted in 1980 yielded no fish.

The earliest water chemistry data for Hovvatn date from 1961. Six pH measurements conducted in the 1960s by E. Snekvik from the DVF indicated pH levels of 4.6–5.1. Hovvatn was included as lake No. 4.1 in a regional survey of 155 small lakes in southern Norway first conducted in October 1974 (Wright and Henriksen 1978) and later repeated in 1975, 1976, 1977, 1978, and 1981. These data show pH 4.3–4.6 in Hovvatn during the 1970s.

Hovvatn's chemistry and fisheries records indicate that it was typical of about 10% of the lakes in southernmost Norway. Of 719 lakes in this area about 10% had pH levels as low or lower than Hovvatn (Wright and Snekvik 1978) and about 8% had lost their fish populations prior to 1950 (Sevaldrud et al. 1980).

In March 1981, 200 metric tons (t) of powdered limestone were spread on the snow in a 10-m-wide, 3-km-long strip along the eastern shore of Hovvatn and around the islands (Fig. 1). An additional 40 t was spread on the ice over the entire Pollen. Spreading was accomplished in two steps. First, a 2-m-wide layer was laid down by a tractor-driven manure spreader. Then, a tractor-mounted snow blower deposited a 10-m-wide cloud of limestone mixed with snow along the shore. Cost of the limestone, transport, and spreading amounted to 1000 NOK/t (equivalent to Can $220/t at 1981 exchange rates).

The limestone was agricultural grade with 90% < 0.1 mm and 50% < 0.01 mm. Its composition was 80% $CaCO_3$ and 14% SiO_2. The liming doses for Hovvatn and Pollen were 0.27 and 1.3 t/ha terrestrial catchment, respectively, which correspond to 25 and 210 g/m^3 lakewater. The dose for Hovvatn was chosen to achieve pH 6–7 and an alkalinity of 50–100 μeq/L after liming and to neutralize an additional 1 yr of acidic runoff. The theoretical requirement to increase alkalinity of 6.4×10^6 m^3 of lakewater by 120 μeq/L (from -46 μeq/L) is 40 t of $CaCO_3$. An additional 40 t is required to neutralize 1 yr of acidic runoff. Liming experiments in Sweden (Swedish National Board of Fisheries 1981) indicated that only 40–50% of the applied limestone could be expected to dissolve within the first 2–3 yr. Thus, 160 t of $CaCO_3$ (equivalent to 200 t of limestone with 80% $CaCO_3$) was chosen as the dose for Hovvatn. The higher

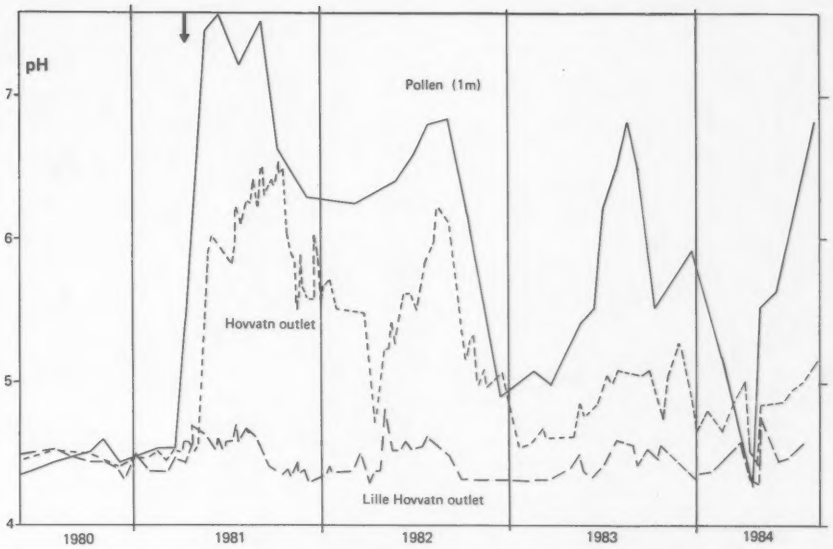

FIG. 2. pH levels in the untreated Lille Hovvatn (outlet), the limed Hovvatn (outlet), and limed Pollen (1 m) over the period May 1980 – August 1984. Liming was conducted in March 1981 (arrow).

dose for Pollen was chosen with the aim of maintaining pH levels above 5.5 for 5 yr. In comparison with similar lake-liming experiments in Sweden (Hultberg and Andersson 1982; Swedish National Board of Fisheries 1981) and Canada (Adamski and Michalski 1975; Dillon et al. 1979; Molot et al. 1984), the dose at Hovvatn was rather modest and that for Pollen rather high.

Methods

Samples for water chemistry were collected about eight times a year at two to five depths from four (later three) stations in Hovvatn, one in Pollen, and (beginning in 1983) one in Lille Hovvatn (Fig. 1). The major inflowing stream to Hovvatn (from Lille Hovvatn) and the outlet of Hovvatn were sampled more frequently.

The samples were collected in polyethylene bottles and stored cool and in the dark during transport to the laboratory at the Norwegian Institute for Water Research in Oslo. Analysis was by routine methods for softwaters. The pH was measured with an Orion 701 meter and Radiometer GK 2301C glass electrode. Specific conductance was determined with a Phillips PW 9501 meter at 20°C. Levels of Ca, Mg, K, and Na were determined by atomic absorption spectrophotometry with lanthanum added to mask interferences. Total Al, SO_4, Cl, NO_3, and NH_4 were determined using automated colorimetric procedures; the catechol violet method (Al), thorin method (SO_4), ironthiocyanate method (Cl), NEDA method (NO_3), and indophenol method (NH_4) were used. Alkalinity was determined by acid titration to pH 4.5 fixed-endpoint and then converted to inflection-point alkalinity using the procedure suggested by Henriksen (1983). Total organic carbon was measured as CO_2 by gas chromatography; total P was measured by UV-oxidation to ortho-P and the molybdate method; total N was determined as NO_3 following UV oxidation.

Beginning in October 1983, analysis for Al fractions was added to the analytical program. In addition to total Al (determined after addition of acid for >3 d), reactive Al (determined immediately after addition of acid), nonlabile monomeric Al, and labile monomeric Al fractions were measured. Driscoll's (1980) ion-exchange procedure modified for autoanalyzer by Røgeberg and Henriksen (1985) was used.

In addition to this routine sampling and analysis program, occasional samples were collected in acid-washed glass vials and analyzed for Fe, Mn, Pb, Cl, Cu, and Zn by atomic absorption spectrophotometry and using a graphite furnace.

Wright and Henriksen (1978) and Henriksen and Wright (1978) gave details for the analytical methods for major ions and heavy metals, respectively. The complete analytical data are listed in Wright (1982, 1984a, 1984b).

Results and Discussion

Water Chemistry

Prior to liming, the chemistry of Hovvatn was characterized by high mineral acidity (pH 4.3–4.5), high Al concentrations, and negative alkalinity with sulfate as the major anion. This chemical composition is typical for Lille Hovvatn, the inflowing streams, and surface waters in much of the region.

In dilute oligotrophic freshwaters the major chemical species governing alkalinity are typically bicarbonate, H^+, and inorganic Al species (Wright 1983):

$$\text{Alkalinity} = HCO_3 - H^+ - \Sigma\,Al$$

where Σ Al denotes the sum of positively charged inorganic Al species in (microequivalents per litre). In practice, if alkalinity is positive, H^+ and Σ Al are negligible, and if alkalinity is negative, HCO_3 is negligible (Wright 1983). Σ Al is important only when pH < 5 and is assumed equal to the difference in measured total Al before and after liming.

As expected, application of limestone resulted in dramatic increases in pH, alkalinity, and Ca and large declines in total Al concentrations (Fig. 2–4). The change occurred within 5 d of ice-out, when the limestone powder on the ice and along the

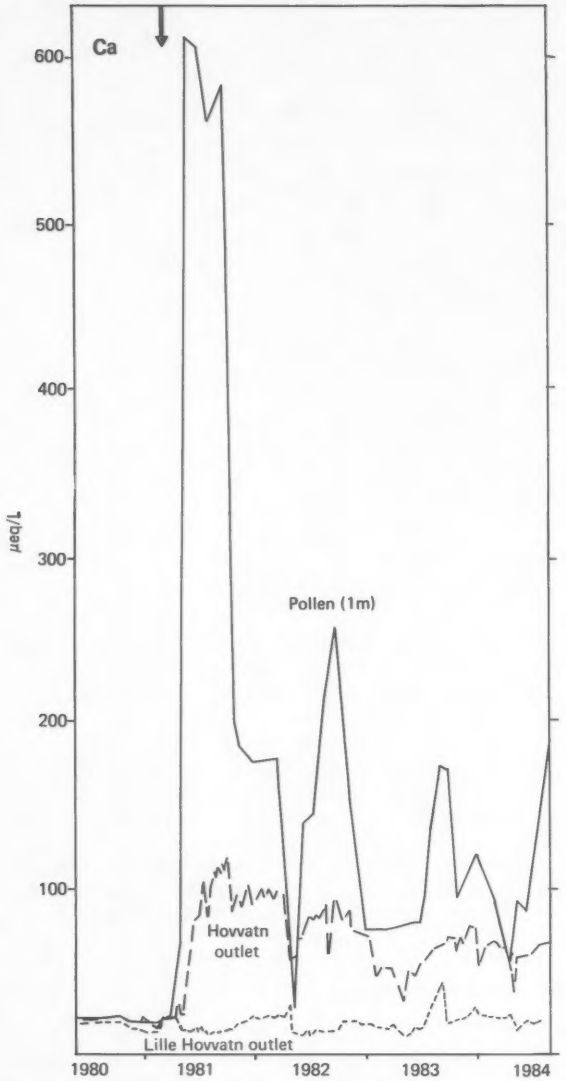

FIG. 3. Concentrations of Ca in the untreated Lille Hovvatn (outlet), the limed Hovvatn (outlet), and limed Pollen (1 m) over the period May 1980 – August 1984. Liming was conducted in March 1981 (arrow).

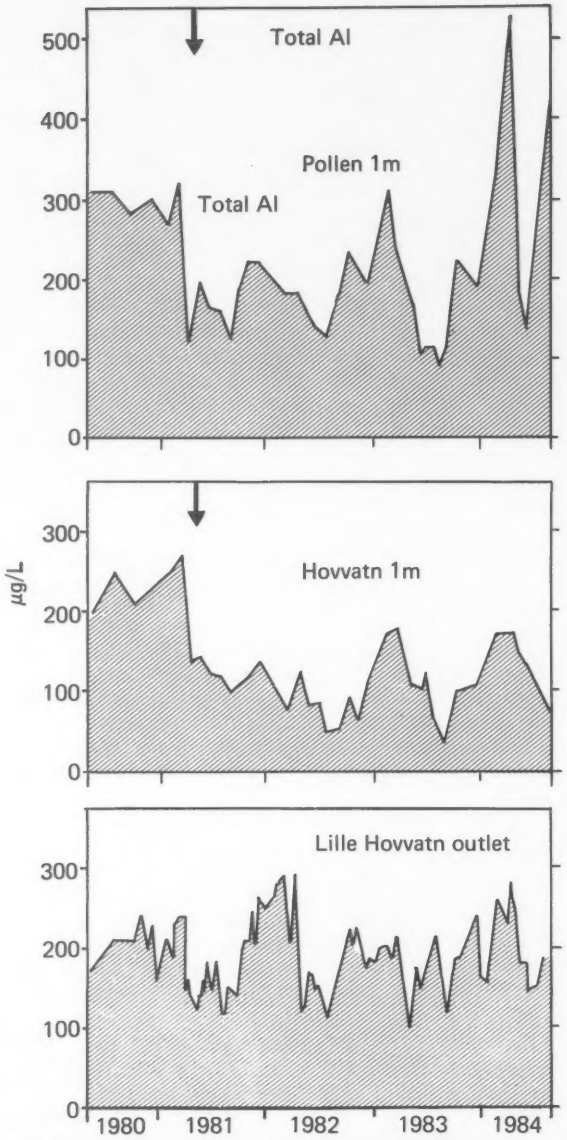

FIG. 4. Concentrations of total Al in Hovvatn (1 m), Pollen (1 m), and Lille Hovvatn (outlet) over the period May 1980 – August 1984. Liming was conducted in March 1981 (arrows).

shores first came in contact with the acidic lake water. The immediate increase in Ca concentrations was from 24 to 64 µeq/L in Hovvatn and to 612 µeq/L in Pollen. The pH increased from 4.5 to 6.4 and 7.4, respectively. Al declined by about 14 µeq/L at both sites. None of the other major ions exhibited significant changes in concentration as a result of liming.

The immediate increase in Ca concentration was equal to increase in alkalinity. In Hovvatn, the 64-µeq/L increase in alkalinity came from a reduction in H^+ concentration of 32 µeq/L, a reduction in Al of 14 µeq/L, and an increase in HCO_3 concentration of 18 µeq/L. In Pollen, the changes in H^+ and Σ Al were as in Hovvatn, but the greater lime dose resulted in a much larger HCO_3 concentration, 543 µeq/L.

The decrease in Al concentration probably resulted from the precipitation of an aluminum hydroxide phase such as microcrystalline gibbsite. The solubility of $Al(OH)_3$ decreases dramatically as pH increases from below 4.5 to above 5.0. A study of Al speciation across the pH gradient at the mouth of the acid stream from Lille Hovvatn out into the limed Hovvatn showed that total Al concentrations decreased with increasing pH, and that Hovvatn at pH 5.4 was slightly oversaturated with respect to microcrystalline gibbsite (Wright and Skogheim 1983).

Precipitation of $Al(OH)_3$ from neutralized lakewater apparently proceeds slowly. Following ice-out in May 1981, pH, Ca, and alkalinity in Hovvatn and Pollen increased immediately as

TABLE 2. Relationships between Al fractions, pH, and TOC at Hovvatn in 69 samples collected during October 1983 – August 1984. Fractions measured are total Al, reactive Al (RAL), and nonlabile monomeric Al (NLAL). Labile monomeric Al (LAL) is determined by difference (RAL − NLAL).

Linear regression	r
RAL (μg/L) = −8 + 0.87 total Al (μg/L)	0.95
NLAL (μg/L) = −23 + 22 TOC (mg/L)	0.89
log LAL (μg/L) = 5.17 − 0.66 pH	0.96
RAL (μg/L) = 40 + 12 TOC + 4 H^+ (μeq/L)	0.89

the limestone came in contact with the water. The levels of total Al in unfiltered water, however, declined slowly over the next several weeks (Fig. 4). Furthermore, Al concentrations exhibited a marked vertical gradient in the water column with higher concentrations in the bottom waters. Slow removal of Al after liming acid water has also been reported from Sweden (Swedish National Board of Fisheries 1981).

Al fractions in water samples collected at Hovvatn over the period October 1983 – August 1984 reveal systematic relationships between the concentrations of nonlabile monomeric Al (NLAL) and total organic carbon (TOC) and between the concentration of labile monomeric Al (LAL) and pH (Table 2; Fig. 5). These relationships are similar to those found by Driscoll (1980) and Driscoll et al. (1984) in acidified waters in the Adirondack region of New York. At Hovvatn the difference between total Al and reactive Al is small (Table 2). Multiple linear regression of reactive Al on TOC and H^+ indicates that 90% of the variance is accounted for by these two factors.

In both Hovvatn and Pollen, alkalinity and Ca concentrations increased further during the first summer after liming to maximum levels in early September, prior to the onset of autumn rains. This indicates that limestone continued to dissolve during the first summer.

Reacidification of Hovvatn and Pollen began with the onset of autumn rains in September 1981. Precipitation and runoff from the terrestrial catchments were, of course, acidic and unaffected by the lime treatment. The effect of the liming decreased in both water bodies as the high-pH, limed water was back-titrated and flushed out by incoming acidic runoff and precipitation. By 25 May 1982, 1 yr after liming, the pH level in Hovvatn had decreased to 5.6 (from a high of 6.7 in September 1981); in Pollen the pH was 6.4 (from maximum 7.5). Ca and HCO_3 levels had also decreased. After 2 yr, 13 May 1983, pH in Hovvatn was 4.9 and 5.4 in Pollen, after 3 yr, pH was 4.9 and 5.6, respectively (Fig. 3).

Liming did not affect the concentrations of the other major ions (Na, K, Mg, NH_4, NO_3, SO_4, and Cl) or the trace metals (Cu, Zn, Cd, Pb, Fe). Mn concentrations appeared to decrease following liming in both Hovvatn and Pollen from concentrations of 10–20 μg/L before liming to 5–10 μg/L by the end of the first summer after liming. Liming experiments in Sweden and Ontario also caused decreases in Mn concentrations; a possible cause may be the co-precipitation with aluminum hydroxides (Dickson 1979; Dillon et al. 1979).

At Hovvatn, there is no evidence that redox reactions in the hypolimnion or sediment surface cause significant changes in SO_4, NO_3, or NH_4 concentrations. Such reactions were observed in several Swedish lakes, both limed and acidic (Hultberg and Andersson 1982). An extreme case is experimentally acidified Lake 223 in the Experimental Lakes Area, northwestern Ontario, where SO_4 reduction in the hypolimnion is a significant source of alkalinity (Schindler et al. 1980). Unlike Hovvatn and the Swedish lakes, however, Lake 223 does not experience complete oxygenation of the hypolimnion during spring turnover, and thus, anoxic conditions are more readily obtained. Measurements of dissolved oxygen concentration in Hovvatn in April 1982, after the winter-long stagnation and just prior to ice-out, showed >50% saturation at all water depths.

TOC, total P and possibly also total N were affected by the

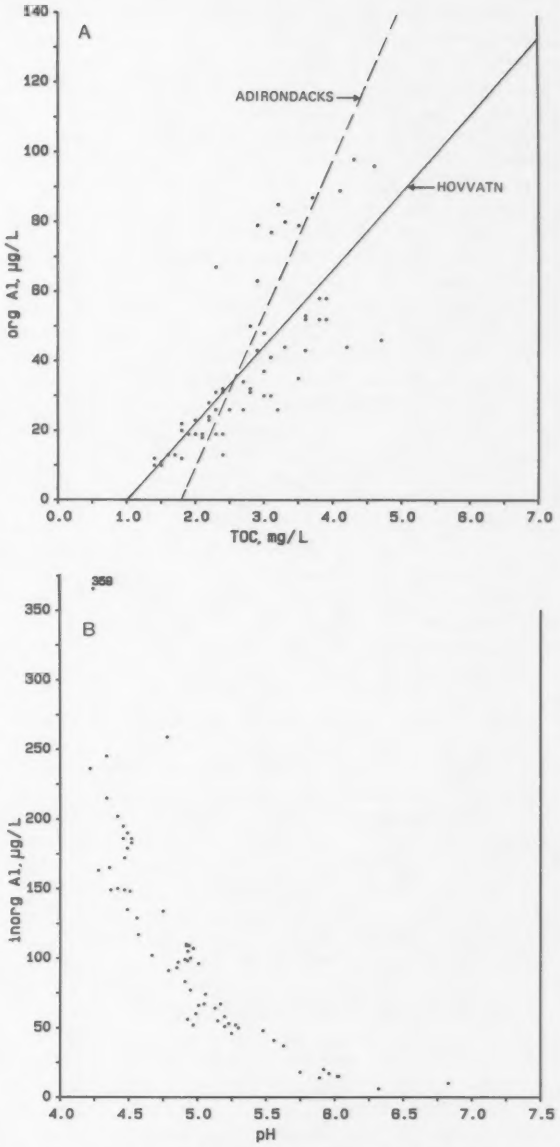

FIG. 5. (A) Relationship between organic Al (nonlabile monomeric Al) and TOC for 69 water samples from Hovvatn collected during October 1983 – August 1984. Least-squares linear regression line for these data and for similar data from 297 water samples from the Adirondack region of New York (Driscoll et al. 1984). (B) Relationship between inorganic Al (labile Al) and pH for Hovvatn.

limestone treatment. TOC levels increased from about 2–3 mg/L before liming to about 4 and 5–8 mg/L in Hovvatn and Pollen, respectively, during the first and second year after treatment. Data for the first half of 1983 indicate that TOC levels had decreased to preliming concentrations (Wright 1984a).

Many studies have shown that liming acidic lakes causes changes in TOC, color, and transparency. Liming with high doses of $CaCO_3$ can result in decreases in TOC and color (transparency increases) apparently due to precipitation of humic substances. Several lakes in Sweden responded in this manner (Swedish National Board of Fisheries 1981; Hultberg and Andersson 1982) as did a lake in the Adirondack Mountains in New York (Driscoll et al. 1982). On the other hand, liming can cause increases in TOC and color and decreases in transparency (Dickson 1979). Mechanisms here include increased phytoplankton growth, increased respiration in the sediment with release of organic substances to the overlying water, and simple pH-dependent light adsorption by humic substances (Hultberg and Andersson 1982; Yan 1983). In Hovvatn, as in several other limed lakes in Ontario (Dillon et al. 1979; Yan 1983), changes in TOC, color, and transparency cannot be explained by changes in the phytoplankton. The changes in TOC, color, and transparency with liming and reacidification are variable and probably due to several factors. As both Hultberg and Andersson (1982) and Yan (1983) pointed out, such changes in transparency influence light penetration, heat balance, and mixing in lakes and may be of biotic significance.

Concentrations of total P in Hovvatn and Pollen increased with liming (Wright 1984a). In Hovvatn the increase was from about 4–5 to 7 μg/L and was only of a few months duration. In Pollen the increase was larger, up to 10–12 μg/L, and was evident during both 1981 and 1982. Increases in P could come from dissolution of trace amounts of P contained in the limestone or from release of P from the sediments as a result of increased respiration. Trace amounts of P in a Swedish limestone amount to about 0.5–1 μg/L per milligrams of Ca dissolved per litre (Swedish National Board of Fisheries 1981). In Hovvatn, Ca concentrations increased about 2 mg/L. Using the Swedish data, an increase of 1–2 μg P/L would be expected, approximately the increase observed. In Pollen the high dose gave a Ca increase of about 12 mg/L, which would correspond to 6–12 μg P/L, again approximately the increase observed. In the liming experiments conducted by Hultberg and Andersson (1982) no P increases were observed, but here, neutralization was with a Ca-silicate industrial waste product that may not have contained soluble P.

The increased P concentrations may, however, be due to release from the lake sediments. Several lines of evidence support this mechanism. (1) The long duration of increased P levels in Pollen suggests a continued supply rather than one-time addition with the limestone. (2) The elevated P levels roughly parallel the elevated TOC levels, with both returning to preliming levels by 1983. If increased respiration in the sediments occurs as a result of liming, then TOC and P might be released together. On the other hand, other liming experiments did not produce increases in total P (Hultberg and Andersson 1982; Eriksson et al. 1983) and a Norwegian study of sediment–water interactions indicated only a minor release of P with liming (Sanni et al. 1983). Furthermore, a laboratory incubation of Hovvatn and Pollen sediments with limed and acidic water also showed only minor release of P from the sediment to overlying water (S. A. Norton and R. F. Wright, unpubl. data). Clearly, further work is necessary before the effect of liming on P concentrations can be satisfactorily explained.

Amount of Limestone Dissolved

The Ca budget for a lake provides the best measure of the amount of limestone dissolved and of the rate of reacidification. The Ca budget consists of the inputs from runoff (includes groundwater) from the catchment and precipitation on the lake surface, dissolution of limestone and release from the lake sediments, and outputs via outlet discharge and via removal from the water to the sediments.

Alternatively, alkalinity could be used because dissolution of $CaCO_3$ by H_2CO_3 produces equivalent amounts of Ca and alkalinity. Alkalinity is, however, more cumbersome a measure because it consists of three components, HCO_3, H^+, and ΣAl, and it would be necessary to assess the fluxes into and out of the lake water for all of these.

For the Ca budgets at Hovvatn and Pollen, fluxes in runoff, precipitation, and outlet discharge are obtained from hydrologic budgets and measured Ca concentrations in stream and lake water. The flux of Ca across the sediment–water interface is estimated from laboratory experiments (S. A. Norton and R. F. Wright, unpubl. data) and also from changes in Ca concentration in bottom water during periods of thermal stratification. The Ca derived from dissolution of limestone is estimated by difference.

For the purpose of assessing the liming efficiency, an adequate hydrologic budget is obtained from measurements of precipitation depth at a station operated by the Norwegian Meteorological Institute (MI) at Dovland, about 10 km south of Hovvatn. Evapotranspiration is assumed equal to 200 mm/yr. Outlet discharge is then obtained by difference:

$$Q = P - ET$$

where P is measured precipitation depth, ET is estimated evapotranspiration, and Q is outlet discharge (units are millimetres). Precipitation in winter comes as snow and runs off during spring snowmelt. Winter baseflow is assumed to be 25–40 mm/mo.

This method produces adequate hydrologic budgets for relatively long periods. The year is divided into four hydrologic periods: summer (ice-out to onset of autumn circulation), autumn (until ice-on), winter (until snowmelt), and spring (snowmelt to ice-out). In addition to these four periods in 1982 a midwinter melting period was added. The hydrologic year used here is thus May to May (ice-out to ice-out).

Of the first 3 full yr since liming, 2 (1981–82 and 1983–84) were hydrologically normal with about 1400 mm of precipitation (30-yr mean = 1460 mm) distributed normally over the year; 1982–83, on the other hand, was substantially wetter (1710 mm) and characterized by a mild winter. Ice-on was not until mid-December, 1 mo later than normal, and in January, rain and high temperatures caused melting of much of the snowpack.

Ca concentration of inflowing water from the catchment to both Hovvatn and Pollen is about 20 μeq/L, the level in both lakes prior to liming, in Lille Hovvatn, and in the inflowing streams. The volume of water flowing into Hovvatn and Pollen is assumed to be equal to that flowing out. The Ca concentration in outflow water for each hydrologic period was set as the mean concentration in the outlet stream (Hovvatn) and at 1-m depths

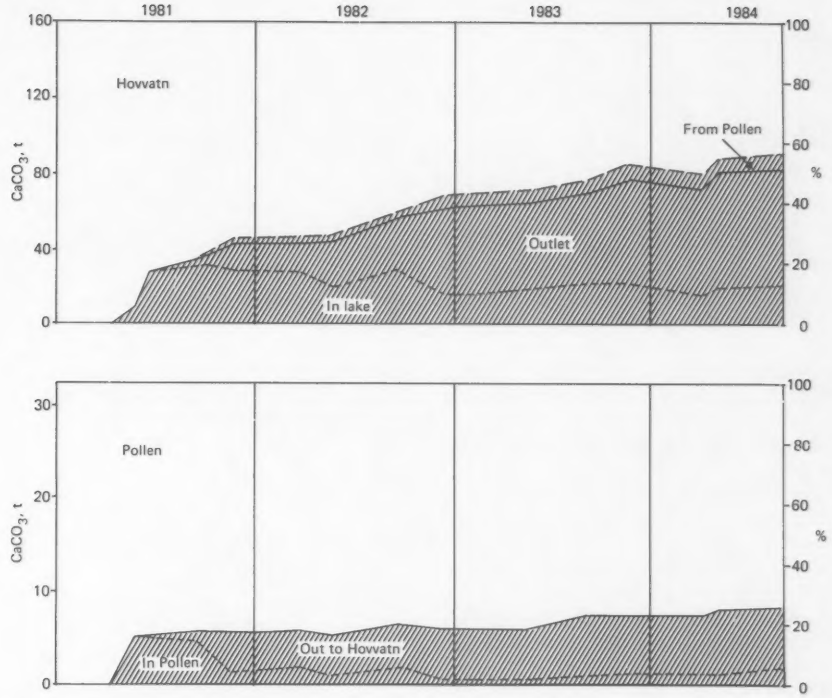

FIG. 6. Cumulative amount of limestone dissolved at Hovvatn and Pollen since liming during March 1981 – August 1984 as calculated from the Ca budgets. Hovvatn receives lime-rich water from Pollen in addition to limestone dissolved in the lake itself.

in Pollen. The change in amount of Ca contained in Hovvatn and Pollen (ΔCa) was estimated from concentrations measured at several depths at the beginning and end of each hydrologic period.

For Pollen, the amount of limestone dissolved during each hydrologic period is then obtained from:

$$\text{Ca dissolved} = \text{Ca out} - \text{Ca in} + \Delta\text{Ca}$$

where ΔCa is the change in Ca contained in the water (concentration $\times$ volume). For Hovvatn, the calculation is similar except that output from the Pollen is an additional input to Hovvatn.

These calculations indicate that in Pollen, 4.4 t of $CaCO_3$ dissolved immediately upon ice-out in May 1981 (14% of the applied limestone) and a further 1.0 t dissolved during the course of the first summer. Since then, further dissolution has been only about 1 t/yr, mostly during the summer. During the rest of the year, dissolution was minimal. By 26 August 1984, about 3.5 yr after the limestone was applied, a total of only 8 t of $CaCO_3$ had dissolved (25%) (Fig. 6).

In Hovvatn, about 22 t of $CaCO_3$ dissolved within a few days of ice-out (14% of applied dose). But in Hovvatn, substantial amounts of limestone have continued to dissolve during the ice-free summers and autumns of 1981, 1982, 1983, and 1984. By 26 August 1984, a total of 66 t of $CaCO_3$ (51% of applied limestone) had dissolved (Fig. 6).

The difference in liming efficiency between Pollen (25% after 3.5 yr) and Hovvatn (51%) is due to the differences in dose (1.3 and 0.27 t $CaCO_3$/ha terrestrial catchment, respectively) and method of application (spread on ice over entire Pollen and spread along one shoreline of Hovvatn, respectively). In Pollen, limestone not dissolved while settling through the water column upon ice-out formed a layer of limestone on the sediment at the bottom. The sediment is organic-rich, fine-grained gyttja. Bjerle et al. (1982) suggested that additional dissolution of limestone in such cases is minimal. Increases in pH and especially Ca concentrations in the bottom water during the summer and winter stratification periods indicate that some of this limestone did dissolve, but even if it is assumed that the 1 m of water over the sediment over the entire Pollen is affected, the total amount of $CaCO_3$ dissolved in the bottom water during the four summers and three winters since liming is only 3 t, about 10% of the limestone dose. This value is similar to that obtained from the Ca budget.

In Hovvatn the situation is different. The 120 t of $CaCO_3$ not immediately dissolved at ice-out in 1981 lies along the sandy northeastern shore and along the shores of islands near the center of the lake. During periods of winds from the southwest these shores are subject to considerable wave action, and the turbulence promotes dissolution of the fine-grained limestone. During the first two summers after liming the shallow water was observed to be cloudy due to suspension of limestone particles.

Dissolution of limestone in Hovvatn proceeds during the ice-free period with, on the average, less limestone dissolved per day in each successive year after liming (Fig. 7). The Ca budget indicates that very little limestone is dissolved during the

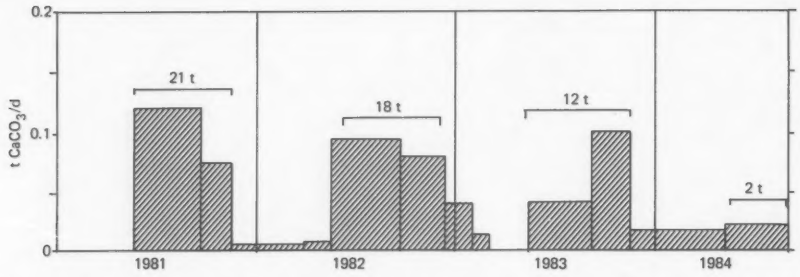

FIG. 7. Dissolution rate of residual limestone at Hovvatn as calculated by difference from the Ca budget (1 t of $CaCO_3$ corresponds to 20 keq of Ca).

winter and during snowmelt. The ice cover would preclude wave action and inhibit dissolution of residual limestone along the shoreline.

The sediments can act as a buffer during liming by taking up Ca from the water (by ion exchange with H^+ on organic materials, for example) and then during reacidification releasing the Ca back to the overlying water (Lindmark 1982; Dillon and Scheider 1983; Sanni et al. 1983). S. A. Norton and I (unpubl. data) conducted in spring of 1983 a series of laboratory experiments with water and sediment from Lille Hovvatn, Hovvatn, and Pollen to assess the importance of sediment buffering. Water from each site was incubated with sediment from each site and the flux of major ions and several trace components measured. This experiment indicated that Pollen sediments will release about 0.7 g Ca/m^2. Extrapolated to the entire Pollen and Hovvatn, these values correspond to about 0.8 and 1.1%, respectively, of the limestone applied.

At neither site is the flux across the sediment–water interface sufficiently large enough to be a significant sink of Ca at liming or a source of Ca during reacidification. The observed chemical changes in Hovvatn bottom water confirm this conclusion. During periods of thermal and chemical stratification, the concentration of Ca in Hovvatn bottom water changes only very slightly, indicating minimal influence of the sediments. The very large changes in Ca concentrations in Pollen bottom water are probably due to dissolution of residual limestone on the sediment rather than interaction with the sediment itself.

Reacidification

Liming raised the pH, alkalinity, and Ca concentration in the lake and Pollen water. Runoff from the catchment was unaffected. Reacidification occurs as the acidic runoff back-titrates and flushes out the limed water. The rate of reacidification depends on the lake's inherent flushing time (volume/outlet discharge), the mixing regime in the lake, and rate of additional dissolution of limestone. With a flushing time of 0.4 yr (Hovvatn 0.8), and only minimal dissolution of residual limestone during the 3.5 yr after application, Pollen should a priori reacidify faster than Hovvatn.

Dimictic lakes such as Hovvatn and Pollen are thermally stratified during summer and winter. During such times, flushing by acidic runoff affects only the epilimnion. The theoretical path of reacidification can be constructed taking into account the observed thermal stratification and flux of acidic runoff from the catchment (Dillon and Scheider 1983). Complete horizontal mixing is assumed. The concentration of Ca is again used as a measure of degree of reacidification.

In the absence of chemical reactions involving Ca (such as dissolution of limestone or release from sediments) the mixing of low-Ca runoff with high-Ca limed water will yield lake water with Ca concentration given by

$$\frac{C_t - C_b}{C_0 - C_b} = e^{-Q/V}$$

where C_t is Ca concentration at time t, C_0 is Ca concentration after liming, C_b is background Ca concentration in runoff, Q is total volume of runoff over the period from time 0 to time t, and V is the volume of lake water mixed.

The volume of the mixed layer varies seasonally. At Hovvatn, spring circulation lasts about 2 wk from ice-out; during this time the entire water column mixes and is subject to reacidification by acid runoff. The mixed volume is thus the entire lake, 6.4×10^6 m^3. Thermal stratification during the summer results in a mixed epilimnion 0–5 m in June, down to 10 m by early August, 15 m in early September, and 25 m in mid-September. The mixed volume during the summer increases from 3.1×10^6 m^3 in June to 6.4×10^6 m^3 at autumn turnover. Autumn turnover lasts until ice-on, usually early November. Under the ice only a 2-m-thick layer is flushed by winter runoff and snowmelt. This volume is only 2.2×10^6 m^3, about one third of the entire lake. At Hovvatn during snowmelt in April 1982, the pH gradient under the ice went from 4.6 at 2 m to 5.2 at 3 m and 5.6 at 5 m. In Pollen the gradient was from pH 4.7 at 1 m to 6.4 at 5 m.

The thermal stratification and resulting changes in mixed volume are similar in Pollen except that (1) the epilimnion is shallower during early summer (Pollen is more sheltered from wind mixing) and (2) Pollen is fully mixed earlier in the autumn because maximum depth is only 9 m.

At Hovvatn, dissolution of residual limestone and incorporation into surface waters during the ice-free periods greatly retards reacidification (Fig. 8). A simple flushing model predicts that Ca levels in surface water should have decreased from initial levels after liming of 90 μeq/L to 50 μeq/L by ice-on in November 1981. In fact, the Ca concentration actually increased to 110 μeq/L during this period, most likely due to dissolution of limestone in the littoral zone during the ice-free period. During ice-covered periods the observed concentrations follow the path predicted by the reacidification model.

The Ca concentration in the bottom water (20-m samples) changes during the spring and autumn circulation periods. During the autumn turnover, the Ca concentration in bottom water increases because during the ice-free period the surface water has acquired Ca from dissolution of residual limestone. During spring turnover, the Ca concentration in bottom water decreases due to dilution with Ca-poor surface water; the

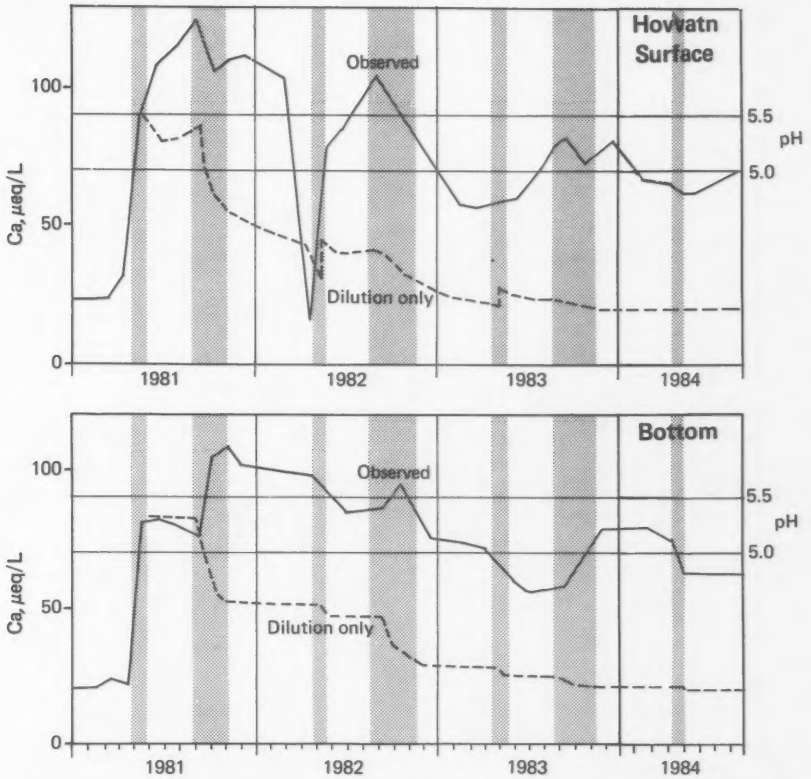

FIG. 8. Reacidification of surface water (1 m) and bottom water (20 m) at Hovvatn during the 3.5 yr since liming in March 1981. Ca concentration is used as a measure of the effect of liming and of reacidification. Background preliming Ca levels were about 20 μeq/L. The broken curves show the expected Ca concentration if the only process occurring is simple flushing of limed water by Ca-poor runoff. Observed Ca levels are higher, indicating significant dissolution of residual limestone after May 1981. During spring and autumn circulation periods (hatched areas) the surface and bottom waters mix to the same chemical composition. Also shown are the Ca levels at which pH drops to 5.5 and 5.0.

surface water beneath the ice has been flushed out by acidic, low-Ca runoff. In the absence of limestone dissolution the Ca concentration in bottom water should follow a step-like path over time with sharp declines during circulation periods and no change during stratification periods. In fact, the steps are up in autumn and down in spring. In between, when the water is thermally isolated, only very slight changes were measured, and these were probably due to Ca release or loss to the sediments.

For Pollen the observed Ca concentrations in surface water (1-m samples) closely follow those predicted by this simple reacidification model (Fig. 9). Observed levels are higher than predicted during the second year after reacidification, but this is due to mixing of Ca-rich bottom water during spring circulation in May 1982. The bottom water (8-m samples) acquired additional Ca from dissolution of residual limestone on the sediments (Fig. 9). Indeed, the Ca concentration in bottom water increases during every period of thermal isolation, and drops due to mixing with reacidification surface water during periods of circulation. Because the volume of the hypolimnion is small relative to the volume of the epilimnion, the effect of dissolution of residual limestone on reacidification of Pollen is minor.

The variations in Ca concentrations over time and with depth are readily translated to pH. Empirically, at a Ca concentration of about 90 μeq/L, pH in Hovvatn is about 5.5, and at 70 μeq/L, it is about 5.0. HCO_3 concentrations become negligible below pH 5.0, and toxic, inorganic forms of Al increase in concentration.

Hovvatn and Pollen had reacidified to pH 4.9 and 5.5, respectively, by spring turnover in 1984, 3 yr after liming (Fig. 2 and 8). Nevertheless, during summer 1984, levels had again risen to pH 5.2 and 6.8, respectively. By then a water volume equivalent to 4.3 times that of Hovvatn and 8 times that of Pollen had entered as acidic runoff and left via the outlets. As of October 1984, reacidification had not yet adversely affected growth or condition of the brown trout stocked annually since liming in 1981 (T. Svälv, Institute of Zoology, University of Oslo, Oslo 3, Norway, unpubl. data). If adverse effects to fish are used as a criterion, then clearly the liming strategies chosen for both Hovvatn and Pollen have been adequate for at least 3.5 yr.

Liming Strategy

The liming strategy at Hovvatn — partial liming along the shores — appears well chosen. After 3.5 yr about 50% of the limestone applied had benefitted the lake. This efficiency

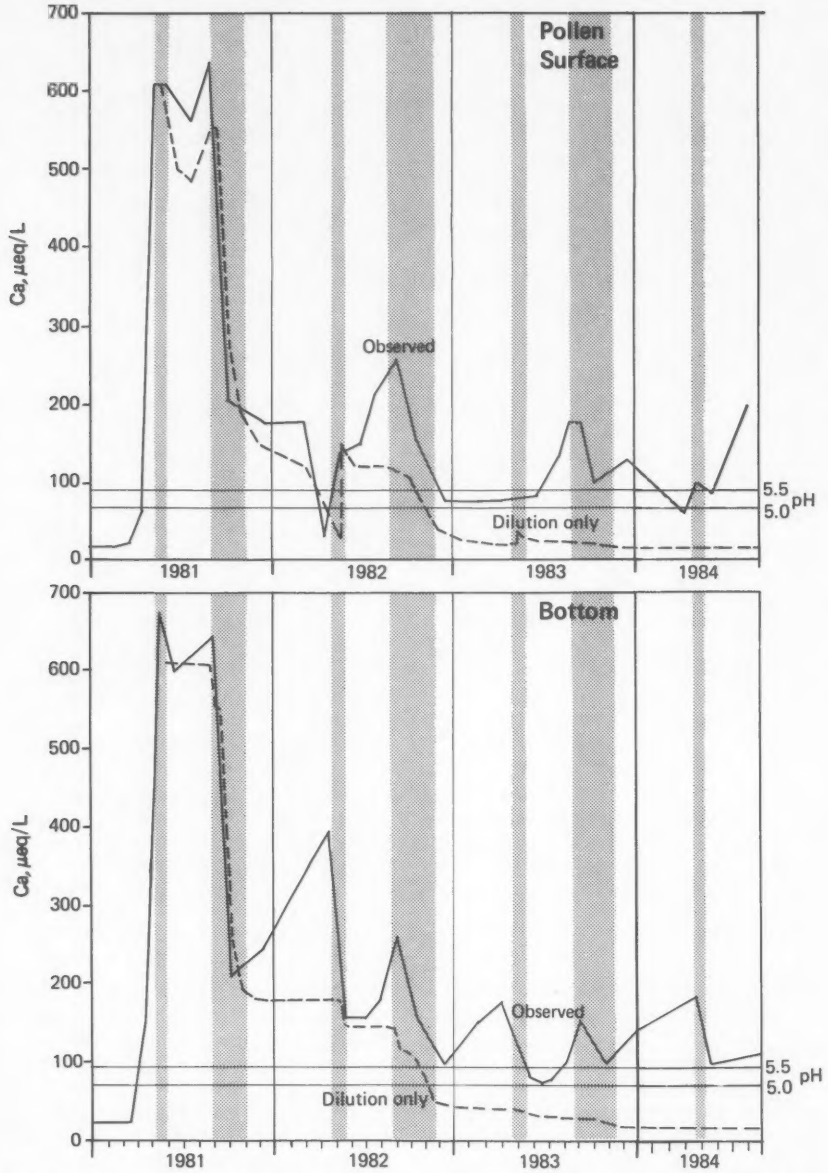

FIG. 9. Reacidification of surface (1 m) and bottom water (8 m) at Pollen during the 3.5 yr since liming (see caption to Fig. 8 for details).

compares favorably with lakes in Sweden and Canada treated with agricultural grade limestone. At Pollen the liming strategy did not result in maximum return. Only 25% of the applied limestone benefitted Pollen. Here, a more moderate dose would probably have had about the same effect.

Dissolution efficiency is not the best measure of successful liming. The ideal dose is one that yields the greatest increase in alkalinity for the greatest length of time at the least cost. Too small a dose may result in 100% dissolution but only a small increase in alkalinity of relatively short-lived duration. Too large a dose causes a large fraction of the limestone to remain undissolved.

As Sverdrup and Bjerle (1983) pointed out, liming efficiency depends on the choice of neutralization material, dose, and application method, and this choice depends, in turn, on the characteristics of the lake to be limed.

At Hovvatn the partial liming strategy creates refugia of acceptable water quality in some parts of the lake during times when other parts of the lake contain more acidic, toxic water. The trout population can then seek out such refugia and survive

temporary pH depressions. Reliming perhaps can be delayed somewhat.

With its small catchment-to-lake area ratio, Hovvatn is somewhat unusual for Norway. Water retention time is about 1 yr, whereas other acidic, barren lakes in the region typically have retention times of 1–6 mo. Whereas liming at Hovvatn has resulted in pH levels above 5 in at least one part of the lake for a full 2 yr (3.2 water retention times), in a lake with a shorter retention time such a liming treatment would have maintained acceptable pH levels for only 1 yr or less. Liming lakes in this part of Norway must therefore be based on annual or biannual treatments. This contrasts sharply with the situation in Sweden and Ontario where due to lower specific runoff rates, the water retention time in acidic lakes is commonly 2–5 yr, and reacidification following liming can take 5–10 yr (Hultberg and Andersson 1982; Dillon and Scheider 1983).

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Planktivory in a Littoral-Dwelling Lake Fish Association: Prey Selection and Seasonality

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A littoral zone assemblage of six planktivorous fishes (*Pimephales notatus*, *Notropis heterodon*, *Fundulus diaphanus*, *Lepomis macrochirus*, *Ambloplites rupestris*, *Perca flavescens*), and five zooplankter species, was analysed relative to three hypotheses concerning prey consumption: (1) Size-dependent predation will operate, as elsewhere. (2) Small-bodied planktivores, unable to handle larger prey, will take the most abundant zooplankter and not show species specialization. (3) The strongly cyclical nature of zooplankton populations will not permit fish species to specialize exclusively on zooplankton; there will be a negative correlation between zooplankton numbers and use of alternative prey, and at this time the planktivores will minimize competition by choosing different alternative prey. The first hypothesis was supported, the second and third partially so. The small specialist planktivores, *P. notatus* and *N. heterodon*, did not take the commonest small zooplankter, *Bosmina longirostris*: rather, they specialized largely on *Chydorus sphaericus*, feeding on it even when rare. *Lepomis macrochirus*, a generalist, took largely *B. longirostris*. No species was exclusively planktivorous. The species only partly differed in alternative prey types eaten. Chironomid larvae were a regular item of diet of most species.

Un regroupement de six poissons planctivores peuplant la zone littorale (*Pimephales notatus*, *Notropis heterodon*, *Fundulus diaphanus*, *Lepomis macrochirus*, *Ambloplites rupestris*, *Perca flavescens*) et cinq espèces de zooplancton ont été analysés en fonction de trois hypothèses sur la consommation de proies : (1) la prédation en fonction de la taille aura lieu comme ailleurs; (2) les planctivores de petite taille, incapables de manger de grandes proies, consommeront le zooplancton le plus abondant et ne montreront pas une spécialisation spécifique; et (3) la nature fortement cyclique des populations de zooplancton ne permettra pas aux poissons de consommer exclusivement du zooplancton. Il y aura ainsi une corrélation négative entre la quantité de zooplancton et la consommation d'autres proies; à ce moment, les planctivores réduiront la compétition au minimum en choisissant d'autres proies. Tandis que la première hypothèse était étayée, les deux autres ne l'étaient que partiellement. Les petits planctivores spécialisés comme *N. heterodon* et *P. notatus* n'ont pas capturé le petit zooplancton plus commun, *Bosmina longirostris*; par contre, ils ont consommé dans une large mesure *Chydorus sphaericus* même quand cette espèce était rare. *Lepomis macrochirus*, un généraliste, s'est nourri en grande partie de *B. longirostris*. Aucune espèce n'était exclusivement planctivore; les espèces ne différaient en partie qu'au niveau des autres genres de proies consommées. Des larves de chironomidés constituaient un élément régulier du régime alimentaire de la plupart des espèces.

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Planktivory is a basic feature of aquatic systems but many aspects of it remain incompletely investigated. The occurrence of size-selective predation by fish has repeatedly been demonstrated (e.g. Brooks and Dodson 1965; Galbraith 1967; Zaret 1980; Eggers 1982). Yet almost all of this work has been carried out on individual fish species, not at the community level. Many planktivorous fishes are of small size, inferring that their potential for size-selective predation is limited. Is feeding in these fish determined simply by prey abundance? Note that Burbidge (1974), in a study of the blueback herring, *Alosa aestivalis*, found that representation of zooplankter species in the fish stomachs corresponded directly to abundance in the environment. Few attempts have been made to investigate the subdivision of the zooplankter resource between the members of fish communities. Zooplankton abundance fluctuates greatly with the seasons (Pennak 1978; Whiteside et al. 1978). How do planktivorous fish respond to this in their feeding? Finally, what alternative foods are chosen by the different planktivorous fish when zooplankter numbers are low?

A study of these questions forms the basis of the present paper. I examined littoral-dwelling association of planktivores and zooplankters in Lake Opinicon, Ontario. The work is framed around three hypotheses:

(1) Larger bodied fish that are able to select prey of optimum size will take the larger zooplankters; that is, size-dependent predation will operate, as elsewhere. This assumes, of course, that zooplankters of a range of body sizes are available.

(2) Small-bodied planktivorous fishes, whose ability to select larger prey is limited by their small mouths (i.e. that are "gape-limited" (Zaret 1980)), will not show size-dependent predation, nor specialize on individual zooplankter species. This is because species diversity is limited at the lower end of the size spectrum (Keast 1980; Mittelbach 1981a).

(3) Since all zooplankter species vary greatly in abundance

seasonally, no fish species can be exclusively planktivorous and each must switch to alternative prey when zooplankton abundance is low. Moreover, it can be expected that the different species will choose different alternative prey at this time, since, when food is short, diet overlaps between fish species are greatly reduced (Zaret and Rand 1971).

In framing the data relative to these hypotheses, focus was on the following tests:

(i) Within planktivorous fish species, smaller individuals should take only the smaller individuals of planktivore species, with the larger members taking both the larger individuals and other larger bodied prey species.

(ii) Small-bodied planktivores will consume the commonest prey species and, after that, select prey of successively lower levels of abundance; they will change diet seasonally according to whichever zooplankter species is most abundant.

(iii) There will be a negative correlation between total zooplankton numbers in the environment and the use of alternative prey by the planktivorous fish species.

Materials and Methods

Lake Opinicon is a 787-ha mesotrophic lake with mean and maximum water depths of 4.9 and 9.2 m, respectively. The work was carried out in 1980 along a 1000-m shoreline section of Cow Island Bay adjacent to the Queen's University Biological Station. Up to a depth of 2 m, the littoral zone becomes lightly to moderately weeded in late summer with the development of *Potamogeton* sp., *Vallisneria americana*, *Najas flexilis*, *N. guadalupensis*, *Ceratophyllum demersum*, *Chara* sp., and some *Myriophyllum exalbescens* and *M. spicatum* (Keast 1984).

Fish were netted between the 17th and 26th of each month, May–August, and between the 11th and 18th in September and October.

The sample times, 08:00–10:00 and 16:00–19:00, coincided with reported fish feeding peaks (Keast and Welsh 1968). The net used was a 50 × 2.0 m bagged seine of mesh size 5 mm. The net ends, held vertically by weighted poles with 75-m-long ropes attached, were positioned by a boat in water 2.0–2.3 m deep. With the aid of the ropes, the net was drawn from a boat to the shore through measured distances. Allowing for curvature, the effective net width was about 30 m.

As the net was pulled inshore, observers walked behind it to ensure that the lead line remained on the bottom and was not lifted by the weeds. The net was not drawn onto dry land but kept in the shallows so as not to harm the fish. After fish were counted and measured, subsamples were selected for stomach content analysis and the rest were returned to the lake.

Objectives of the fish netting were to sample all of the species and age-classes occurring in the littoral section, and obtain data on feeding. Ages were based on previous determinations (Keast 1977a, 1977b, 1978) and unpublished data.

Whilst in the case of the larger bodied species it was convenient to divide fish up by year-classes, this was not so with the short-lived, smaller bodied bluntnose minnow (*Pimephales notatus*), blackchin shiner (*Notropis heterodon*), and eastern banded killifish (*Fundulus diaphanus*). For these, an arbitrary division of "less than" and "more than" 45 mm total length was used. The former approximated to the limits of the year 0 size-class for July–October and the early year I in May and June. The mesh size used largely excluded individuals of less than 25 mm total length, and hence, this can be regarded as the minimum size limits.

Standard procedures were followed in carrying out the stomach content analyses (Keast 1978). Data for each fish were developed on the basis of percent volumes and numbers of each taxonomic category. The former were used to compare the proportions of nonplanktivorous and planktivorous feeding. The zooplankton portion of the diet was detailed on the basis of numbers of each zooplankter species eaten.

The zooplankton resource was sampled with a 30-L Schindler plankton trap. Samples were taken at 2-wk intervals (12–16th and 24–29th of each month). One set was taken from the water column in water 1.3–1.8 m deep, and with the development of the macrophytes in June, a second series was taken from within the beds in water 1.0–1.5 m deep. The sampling was carried out at dusk when zooplankters tend to concentrate in the upper part of the water column (Meyers 1980) and extended over 5-d periods. The Schindler method is not ideal in vegetation, since one zooplankter, *Sida crystallina*, clings to the vegetation (Fairchild 1981) and hence will be undersampled. However, *S. crystallina* was not a major prey here.

Zooplankton counts were made by the method of Allanson and Kerrich (1961), the samples being diluted in a 250-mL multisided Virtis flask fitted with an electric stirrer. When full mixing had been achieved, three 5-mL subsamples were withdrawn per sample by wide-mouthed pipette and counted. Body length measurements, to provide data on size distribution, are based on subsamples of each species. For making comparisons of plankton availability and fish feeding, the two sets of plankton data for each month were later combined.

Weights of cladocerans of different sizes, for seasonal comparisons with weights of chironomid larvae in the benthos, are based on previously obtained weight–length relationships and abundance data derived as part of this study.

Data on chironomid larvae in the zoobenthos are based on series of 25 × 225 cm^2 samples taken by Ekman grab mounted on a pole. The specimens were taken in the early morning and late afternoon and over 3- to 4-d periods (Keast 1985). The samples were washed, towel-dried, and wet-weighed.

Results

Bluntnose minnow, blackchin shiner, and killifish were represented by adults and juveniles. The first two species were present all summer. Killifish were absent in June and July (Fig. 1). Five year-classes of bluegill (*Lepomis macrochirus*) were present but the majority were less than 88 mm in length (years 0–II) (Fig. 2). Bluegill was the most common species, outnumbering the next commonest species, the bluntnose minnow and blackchin shiner, by two to three to one. Rock bass (*Ambloplites rupestris*) and yellow perch (*Perca flavescens*) were limited to small numbers of year 0 and some year I individuals.

Five cladoceran species of zooplankton made up the bulk of individuals eaten: *Bosmina longirostris*, *Chydorus sphaericus*, *Sida crystallina*, *Simocephalus vetulus*, and *Polyphemus pediculus* (Fig. 1 and 2). Small numbers of the larger bodied offshore species, *Ceriodaphnia lacustris* and *Daphnia retrocurva*, as well as *Eurycercus* sp., *Alona* sp., *Diaphanosoma brachyurum*, and *Acroperus harpae*, were also taken.

Bosmina longirostris was by far the most abundant species. Numbers trapped in May were 10 times those of *C. sphaericus* at its most abundant (August); when *B. longirostris* was least abundant its numbers still equalled those at the peak of *C. sphaericus* (Fig. 3). Other species were uncommon.

The bulk of *B. longirostris* were in the 0.20- to 0.39-mm length range except in May and September when larger indi-

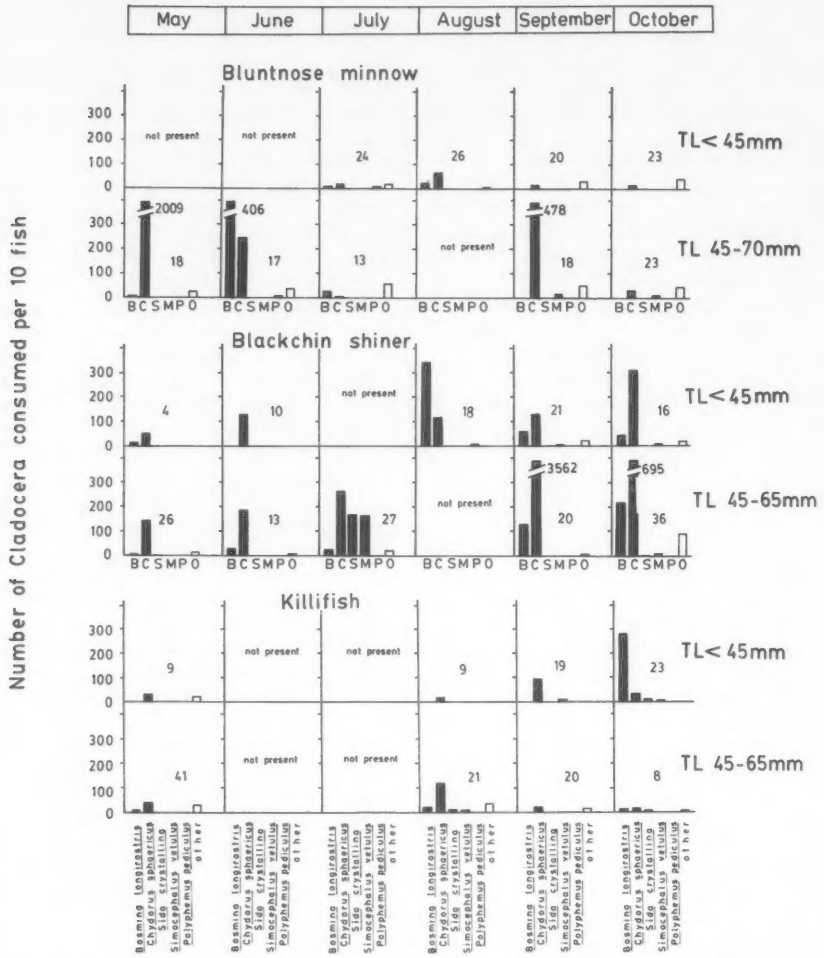

FIG. 1. Species and number of Cladocera found in stomachs of two size-classes of bluntnose minnow, blackchin shiner, and killifish, May–October 1980, in Lake Opinicon. Number of fish stomachs examined is given.

viduals predominated (Fig. 3). Virtually all *C. sphaericus* were in the 0.20- to 0.39-mm length category. Most *S. vetulus* measured 0.30–0.59 mm, *S. crystallina* 0.40–1.5 mm, and *P. pediculus* 0.40–0.79 mm.

Seasonal fluctuations in numbers were as follows. In May, numbers of *B. longirostris* exceeded 10 000 individuals/30 L; there was a second peak in July when numbers rose to greater than 1 000. June and August were periods of low population numbers, abundances being, respectively, about 1/15 of the May population and 1/5 of the July population.

Numbers of *C. sphaericus*, *S. crystallina*, and *P. pediculus* varied seasonally through a factor of 10 and *S. vetulus* a factor of 40.

The zooplankter support base thus showed striking seasonal numerical fluctuations. *Bosmina longirostris*, because of its large numbers, had a dominant role in setting this pattern.

Zooplankton Consumption by the Fish

The various species and age-classes of fish differed considerably in their degree of dependence on zooplankton. Bluntnose minnow and blackchin shiner were specialized planktivores (Table 1; Fig. 1). Killifish took moderate to large amounts of zooplankton. The smallest bluegill were strongly planktivorous, and this decreased as age of fish increased (Table 1; Fig. 2). The year I and II rock bass and yellow perch took only small amounts of zooplankton except in late summer (Fig. 2). Species diets were as follows.

Bluntnose minnow (Fig. 1)

Both size groups of the bluntnose minnow were almost entirely planktivorous (Table 1). *Chydorus sphaericus* was the main zooplankter taken (Fig. 1). It was eaten irrespective of abundance but the largest numbers were taken when populations peaked (Fig. 3). Only in two series (June and July, the larger sized fish) did *B. longirostris* replace *C. sphaericus* as the main prey item. The bluntnose failed to respond to the high abundance levels of *B. longirostris* in May; large-sized zooplankters predominated at this time, however (Fig. 3). *Simocephalus*

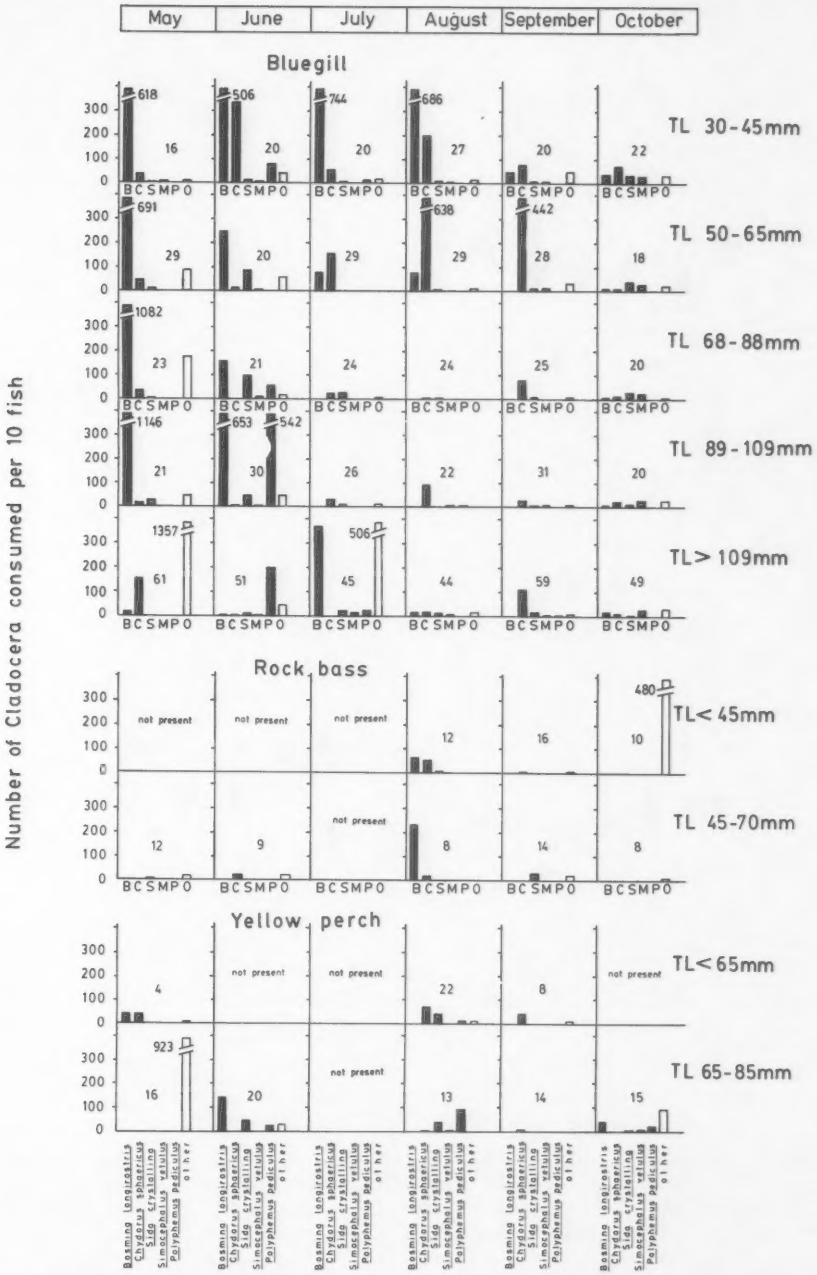

FIG. 2. Species and number of Cladocera found in stomachs of five size-classes of bluegill and two size-classes of rock bass and yellow perch, May–October, in Lake Opinicon. Number of fish stomachs examined is given.

vetulus, a large-bodied species, peaked numerically in June; it likewise was not cropped (Fig. 3).

Some *P. pediculus* and *C. lacustris* were eaten in May and June, *Eurycercus* sp. and *C. lacustris* in July, and *S. vetulus*, *Alona* sp., and *Acroperus harpae* in September and October. Increased consumption of *P. pediculus* in June corresponded to a numerical peak in this species (Fig. 3).

Emphasis was on small-bodied zooplankters: *C. sphaericus* of 0.20–0.29 mm with some 0.30–0.39 mm and *B. longirostris* of 0.30–0.49 mm (Fig. 4 and 5). The mouth of the bluntnose is very small, with an internal width of 0.8–1.3 mm in the smaller, and 1.5–2.4 mm in the larger fish (Keast 1985). Nevertheless, consumption of zooplankter prey of size larger than that consumed should have been possible.

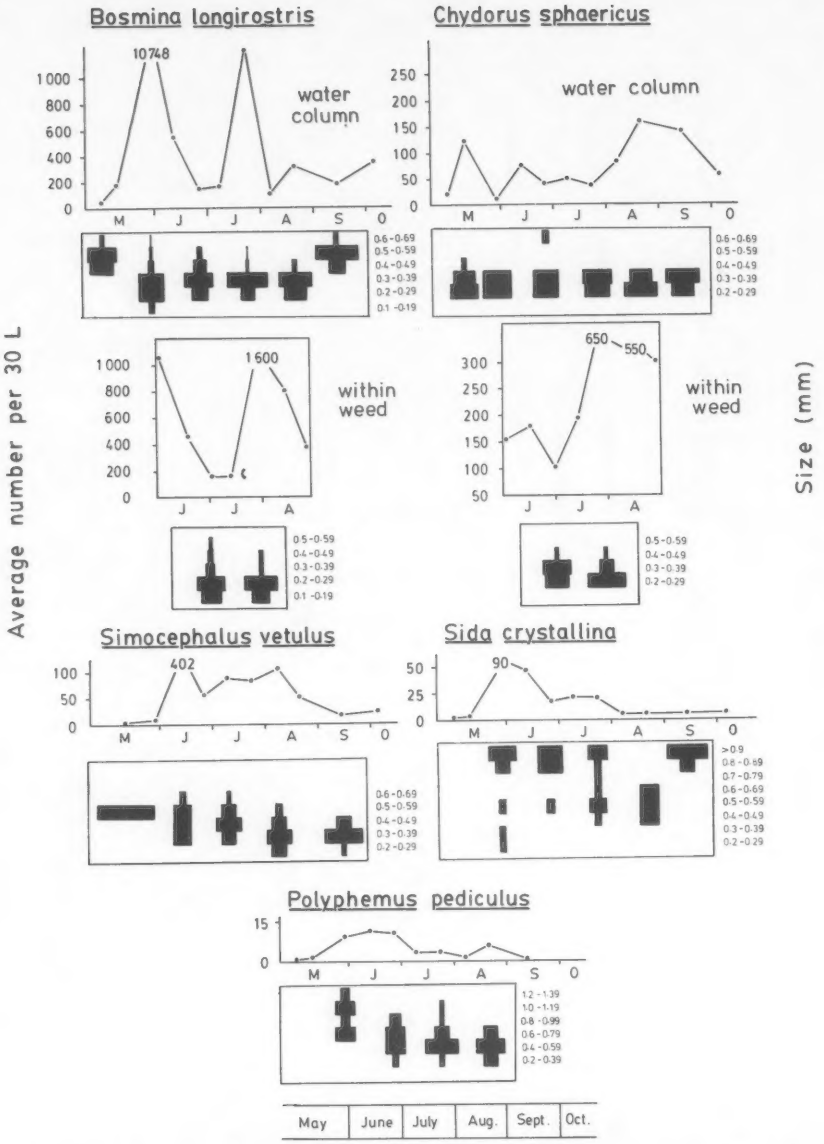

FIG. 3. Abundances and body size distributions of five common cladocerans in Lake Opinicon, May–October. Densities are given for the open water column for all five species, at monthly intervals, and within weed beds for *B. longirostris* and *C. sphaericus* during their June–August period of development.

Chironomid larvae formed an important accessory food of the bluntnose minnow, especially of the older fish, making up 9–26% of stomach content volume per month. Two-thirds of these were in the 1- to 4-mm length range and the remainder were in the 5- to 8-mm range. Consumption patterns showed that they were not eaten when Cladocera were unavailable but represented a regular item of diet (see Fig. 8).

Blackchin shiner (Fig. 1)

The younger age group was overwhelmingly planktivorous, the larger size group less so. Even in the latter, zooplankton exceeding 60% of stomach content volume in 4 of 5 mo.

Chydorus sphaericus was the major zooplankter eaten, and again they were taken irrespective of level of abundance (Fig. 1 and 3). In July when numbers of *C. sphaericus* were low the larger fish consumed significant numbers of *S. vetulus* and *S. crystallina* (Fig. 3). Numbers of the former were high at this time. Almost all zooplankters eaten were 0.29–0.49 mm in length (Fig. 4 and 5). The *S. crystallina* and *S. vetulus* were larger, 0.50–0.69 mm (Fig. 6 and 7). Both size groups of fish

TABLE 1. Diets of the species and age (body size) classes of fish, May–October, based on percent volume of stomach contents, to show importance of zooplankton relative to major alternative or supplementary prey in the diets. Only prey types that exceed 20% by volume of the diet in at least 1 mo are shown. For sample sizes, see Fig. 1 and 2. L = larvae; P = pupae; N = nymphs.

Predator	Prey	May	June	July	Aug.	Sept.	Oct.
Bluntnose minnow							
<45 mm	Zooplankton	—	—	70	83	93	94
	Chironomids (L)	—	—	26	16	5	3
45–70 mm	Zooplankton	48	44	58	—	76	73
	Chironomids (L)	24	26	14	—	9	20
Blackchin shiner							
<45 mm	Zooplankton	—	80	—	90	73	94
45–65 mm	Zooplankton	38	75	60	—	93	88
	Chironomids (L)	18	18	8	—	0	0
	Chironomids (P)	36	6	9	—	0	0
Banded killifish							
<45 mm	Zooplankton	10	—	—	18	82	82
	Chironomids (L)	30	—	—	44	11	7
	Chironomids (P)	15	—	—	10	5	5
45–65 mm	Zooplankton	28	—	—	65	20	20
	Chironomids (L)	24	—	—	15	25	36
	Chironomids (P)	0	—	—	0	18	0
	Diptera adults	0	—	—	0	18	0
	Amphipoda	0	—	—	0	0	20
Bluegill							
30–45 mm	Zooplankton	66	73	42	72	78	68
	Chironomids (L)	15	20	30	15	4	15
50–65 mm	Zooplankton	48	65	26	60	48	50
	Trichoptera	14	3	19	3	4	12
	Chironomids (L)	16	20	18	17	8	10
68–88 mm	Zooplankton	26	33	15	14	22	26
	Trichoptera	5	4	28	15	13	19
	Chironomids (L)	19	30	18	12	17	28
	Ephemeroptera (N)	25	2	4	0	0	0
	Amphipoda	7	0	3	17	7	14
89–109 mm	Zooplankton	20	32	27	16	18	12
	Trichoptera (N)	4	17	15	6	5	11
	Chironomids (L)	25	19	16	30	20	24
	Ephemeroptera (N)	22	0	6	0	0	4
	Amphipoda	3	0	28	13	14	24
>109 mm	Zooplankton	30	20	18	8	8	9
	Trichoptera (N)	2	17	12	4	8	12
	Chironomids (L)	30	18	16	12	16	22
	Ephemeroptera (N)	10	15	3	0	0	3
	Amphipoda	8	3	7	5	19	24
	Plant material	6	10	11	26	23	11
Rock bass							
<45 mm	Zooplankton	—	—	—	25	52	23
	Chironomids (L)	—	—	—	28	24	9
45–70 mm	Zooplankton	18	—	—	21	10	34
	Anisoptera (N)	21	—	—	15	26	0
	Amphipoda	0	—	—	17	24	37
Yellow perch							
<65 mm	Zooplankton	8	—	—	80	8	—
	Chironomids (L)	35	—	—	27	10	—
	Ephemeroptera (N)	0	—	—	0	30	—
	Ostracoda	13	—	—	41	0	—
65–80 mm	Zooplankton	23	42	—	70	20	25
	Chironomids (L)	30	0	—	11	0	12
	Isopoda	34	0	—	0	0	11
	Anisoptera (N)	0	0	—	0	24	0
	Zygoptera (N)	0	30	—	11	30	0

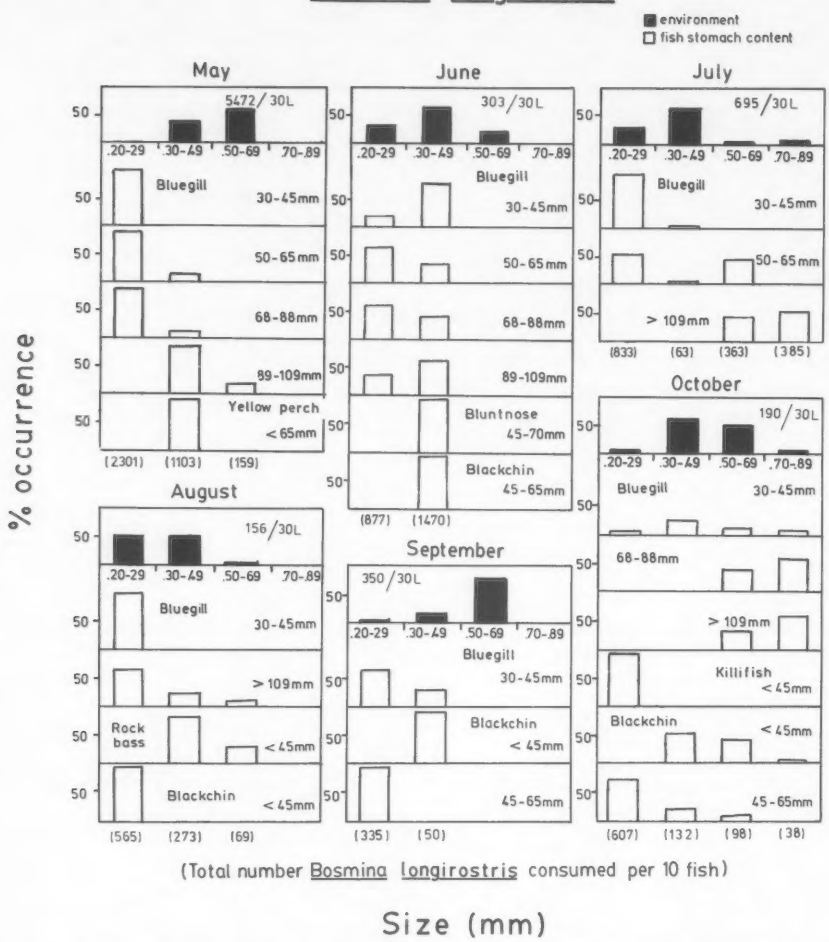

FIG. 4. Occurrence (% total number) of various sizes of *B. longirostris* in the environment (black bars) and in the stomachs of different size-classes of five fish species (open bars) in the inshore area of Lake Opinicon, May–October. Average number of *B. longirostris* occurring per 30 L in the environment is shown on the top right of each monthly histogram. The total number consumed by 10 fish of each species (summed) is given in parentheses at the bottom of the histograms.

chose most prey in the smaller size range. The mouth is also small in this species: 1.2–1.5 mm in the smaller fish and 1.3–2.1 mm in the larger ones (Keast 1985). The zooplankters eaten thus had a body length up to about half the mouth width of the fish.

Chironomid larvae and pupae formed an alternative food of the larger fish in May and June (Table 1; Fig. 8). May was also a time of high *C. sphaericus* populations. Thus, consumption of chironomids did not occur only when *C. sphaericus* was in low numbers. Most chironomids eaten were in the 1.0- to 4.0-mm length range.

Killifish (Fig. 1)

This species was a generalist feeder, not a specialized planktivore. Zooplankton usually accounted for less than 25% of stomach content volume; chironomid larvae and pupae made up 50% (Table 1; Fig. 8). *Chydorus sphaericus* and *B. longirostris* were the most regularly eaten planktivores. Zooplankter prey of a wide range of sizes was taken, including *B. longirostris* as small as 0.20–0.29 mm (October) and *S. vetulus* as large as 0.70–1.20 mm (May, August) (Fig. 4 and 7). This agrees with the slightly larger mouth of the killifish: width 1.3–1.9 mm in the smaller and 1.8–2.7 mm in the larger individuals (Keast 1985 and unpubl. data).

Bluegill (Fig. 2)

The 30- to 45-mm bluegill were largely planktivorous, zooplankton making up 70% (40–80%) of stomach content volumes (Fig. 2; Table 1). Consumption was only partly influenced by level of abundance. In the year I fish, zooplankton consumption fell to about 50%, in year II to 20%, and in year III to 5–10%.

Bosmina longirostris, the commonest species (Fig. 3), was the major zooplankter eaten. Numbers eaten were large. During the May peak of abundance, numbers of *B. longirostris* in the stomachs reached 1000 per 10 stomachs; at other times they reached 500 per 10 stomachs. The species responded strongly to

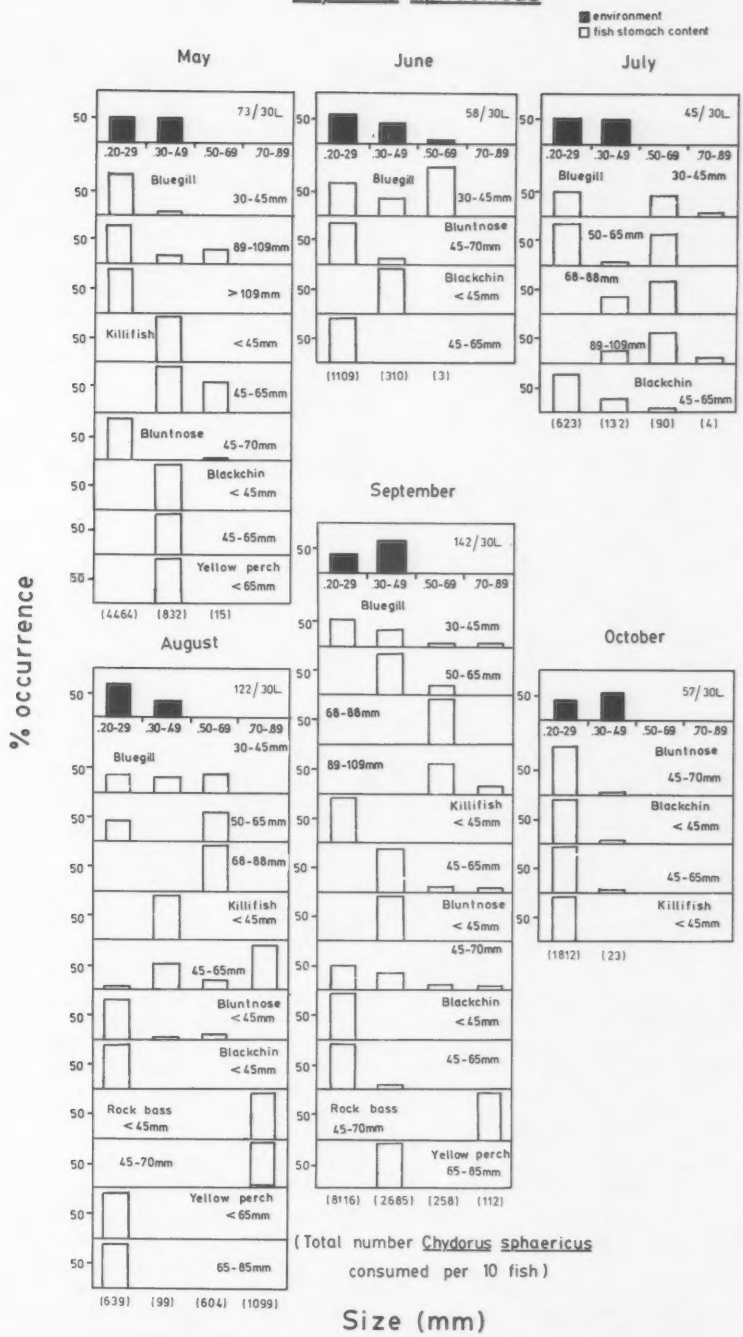

FIG. 5. Occurrence (% total number) of various sizes of *C. sphaericus* in the environment (black bars) and in the stomachs of different size-classes of five fish species (open bars) in the inshore area of Lake Opinicon, May–October. Average number of *C. sphaericus* occurring per 30 L in the environment is shown on the top right of each monthly histogram. The total number consumed by 10 fish of each species (summed) is given in parentheses at the bottom of the histograms.

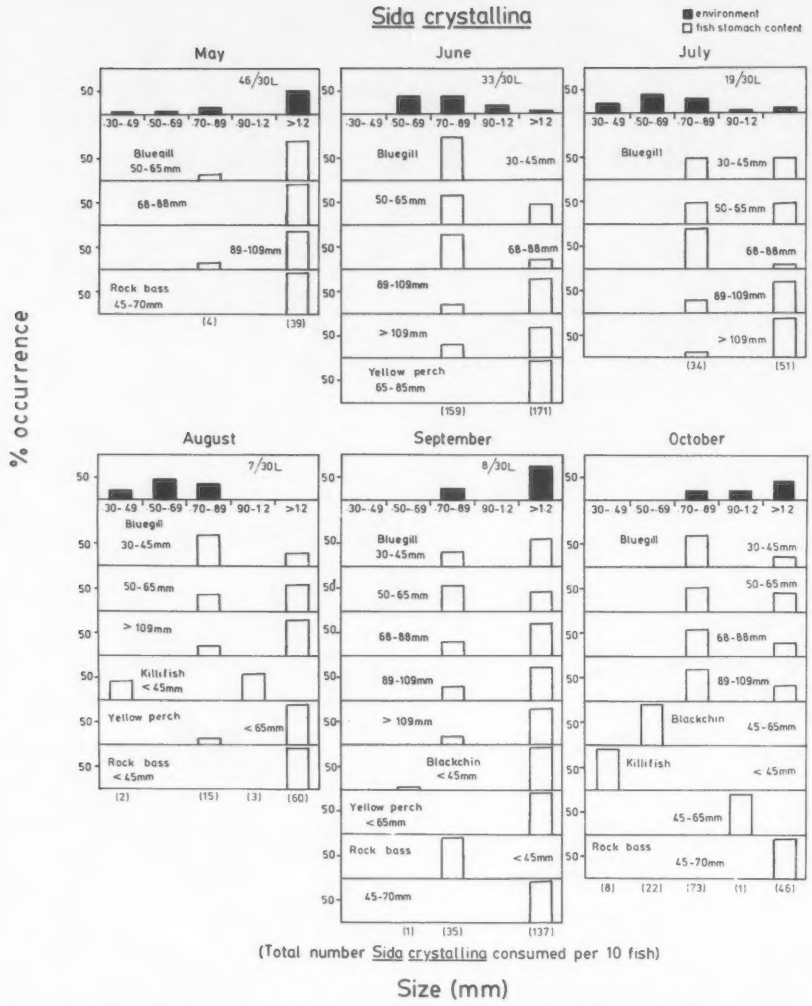

FIG. 6. Occurrence (% total number) of various sizes of *S. crystallina* in the environment (black bars) and in the stomachs of different size-classes of five fish species (open bars) in the inshore area of Lake Opinicon, May–October. Average number of *S. crystallina* occurring per 30 L in the environment is shown on the top right of each monthly histogram. The total number consumed by 10 fish of each species (summed) is given in parentheses at the bottom of the histograms.

the May abundance peak but failed to respond to the July one, when numbers were only about 1/10 those in May. The large (0.40–0.59 mm) *B. longirostris* predominated in May; in July the dominant size was only 0.20–0.39 mm (Fig. 3). In July, bluegill fed heavily on Trichoptera larvae, chironomid larvae, and amphipods (Table 1).

The year I (50–65 mm) bluegill consumed large numbers of *C. sphaericus* in August and September, during the autumn population peak of this species (Fig. 3). Numbers of *B. longirostris* were low then, having fallen to about one-fifth the July numbers. However, its numbers were still no lower than those of *C. sphaericus*.

Polyphemus pediculus was a major diet item of four of the age groups, especially the larger ones, in July (Fig. 2); at this time, populations of this 0.4- to 0.99-mm organism peaked. Its population size nevertheless remained very much smaller than that of *B. longirostris* and *C. sphaericus*. Active selection is indicated. *Sida crystallina* was a minor but important item of diet of the years I, II, and III bluegill in June when numbers of this species were apparently highest (Fig. 3).

There was a clear correlation between size of zooplankter eaten and size of fish. The year 0 fish selected *B. longirostris* in the 0.20- to 0.49-mm length range. By contrast, the year III fish fed largely on 0.50- to 0.89-mm individuals. The *C. sphaericus* eaten were in the 0.50- to 0.69-mm size range, with even the smaller fish taking these (Fig. 5). Bluegill thus selected for larger *C. sphaericus* than did the two cyprinids. All the *S. crystallina* eaten were 0.70–0.89 mm or above (Fig. 6). Some *S. vetulus* 0.50–0.69 mm were eaten but the majority were 0.90–1.2 mm or larger (Fig. 7). Even the 30- to 45-mm bluegill sought large individuals.

The bluegill has a larger mouth width: year 0, (30–45 mm),

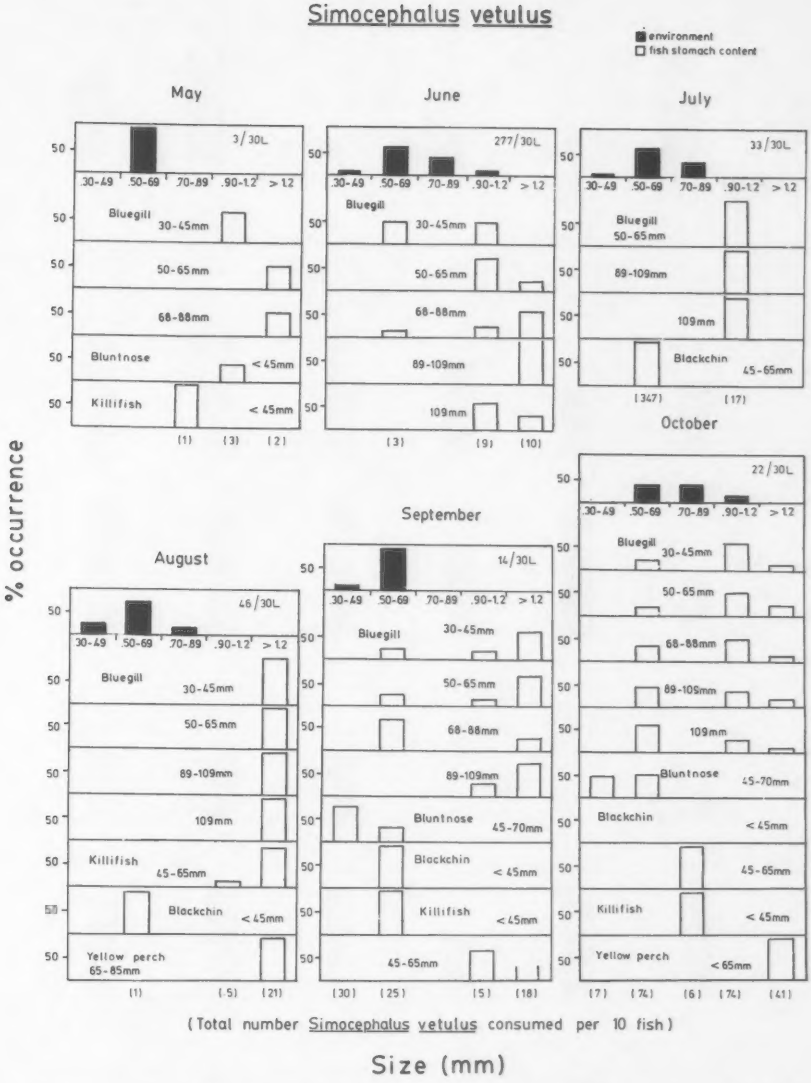

FIG. 7. Occurrence (% total number) of various sizes of *S. vetulus* in the environment (black bars) and in the stomachs of different size-classes of five fish species (open bars) in the inshore area of Lake Opinicon, May–October. Average number of *S. vetulus* occurring per 30 L in the environment is shown on the top right of each monthly histogram. The total number consumed by 10 fish of each species (summed) is given in parentheses at the bottom of the histograms.

1.4–2.4 mm; year I, 2.1–3.7 mm; year II, 3.0–5.0 mm; year III, 4.8–5.9 mm (Keast 1985 and unpubl. data).

The bluegill was primarily a predator on small insects. The year 0 fish supplemented their zooplankton diet with chironomid larvae (Table 1; Fig. 8). Chironomid and Trichoptera larvae dominated the diet of the year I fish. Diet diversity increased with age. Except for the year 0 fish, which are probably limited to cladocera by their small mouth size, feeding on zooplankton occurred mainly when the resource was abundant and individuals of the right size were available. This pattern contrasts with that in the cyprinids. The finding that the bluegill selects for larger zooplankters agrees with the findings of Werner and Hall (1974) and others.

Rock bass (Fig. 2)

Zooplankton usually made up less than 25% of stomach content volumes in year 0 and I fish. Major prey was *B. longirostris* and some *C. sphaericus* in August, *S. crystallina* in September, and *Eurycercus* sp. and *D. retrocurva* in September and October. The zooplankton eaten were of large size: e.g. *B. longirostris*, 0.30–0.69 mm; *C. sphaericus*, 0.60–0.99 mm; *S. crystallina*, 0.70–1.2 mm; *D. retrocurva*, 0.8–1.4 mm (Fig.

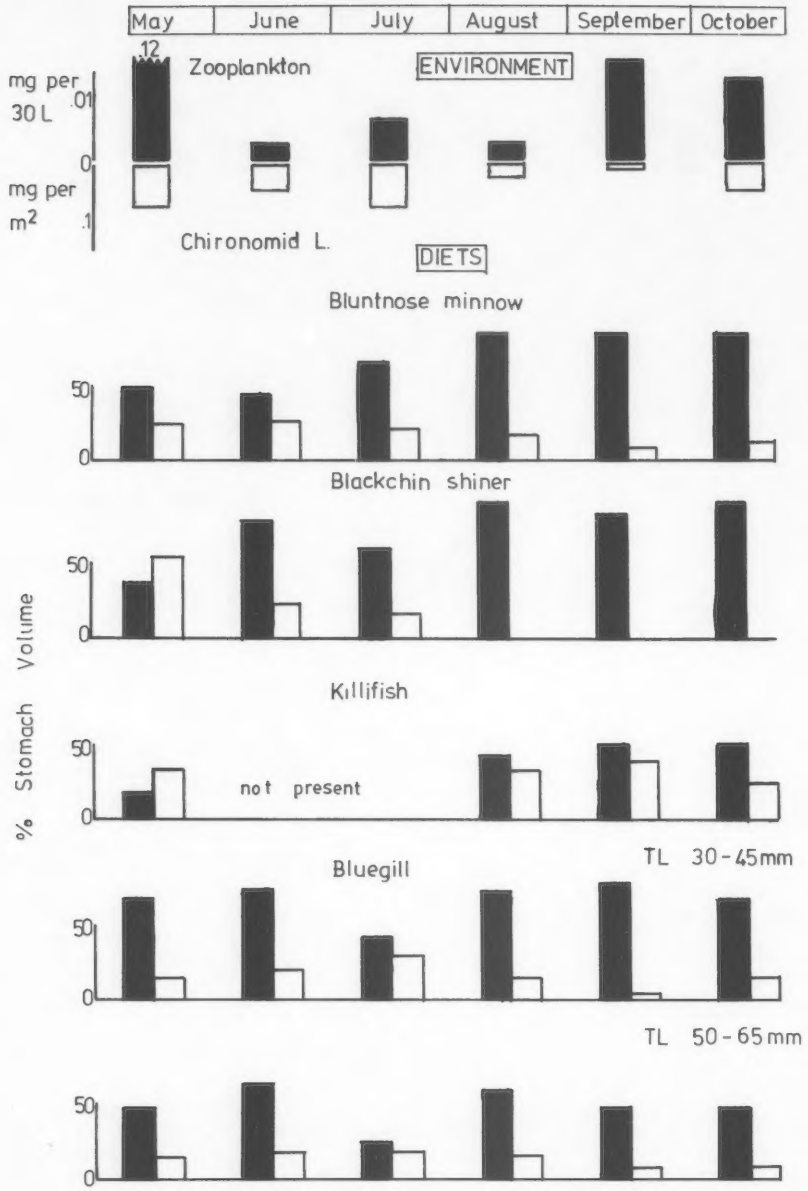

FIG. 8. Percentage wet weights (calculated) of zooplankton (mg/30 L) and chironomid larvae (mg/m^2 of zoobenthos), May–October, compared with percent volumes of these two divisions of prey in the stomachs of the bluntnose minnow, blackchin shiner, killifish, and year 0 and I bluegill. Note that since the zooplankton counts are based on volumes of water and chironomid counts on area of benthos, the two are not directly comparable and can only be used to compare seasonal abundances.

4–7). The rock bass has a large mouth: widths of the two age-classes were 3.0–3.6 and 3.5–6.0 mm (unpubl. data). Planktivory is important only in the youngest rock bass (Table 1).

Yellow perch (Fig. 2)

Zooplankton exceeded 25% of stomach content volume only in August (both size groups of fish) and June (year I fish). Major prey eaten by year 0 fish were *B. longirostris* and *S. crystallina* and by year I fish were *B. longirostris*, *S. crystallina*, *P. pediculus*, and *S. vetulus* (Fig. 4–7). They ranged in size from 0.30 to 1.2 mm, the larger organisms predominating. The diet of yellow perch was diversified (major prey of year 0 fish were chironomid larvae, ostracods, and Ephemeroptera nymphs) and became increasingly so with age (Table 1). Mouth width in the yellow perch was 1.7–2.7 mm in year 0 and 3.0–6.0 mm in year I fish (Table 1). Planktivory in this species is limited and hence

the species contributes little to the resolution of the three hypotheses.

Discussion

Planktivory, in this inshore association, is arranged around three different feeding strategies. There were two specialized planktivores (bluntnose minnow, blackchin shiner), species that are planktivorous mainly at the early juvenile stage (bluegill), and species in which planktivory is opportunistic (killifish, large bluegill), zooplankton being only part of a spectrum of prey types eaten. This finding somewhat confuses the assessment of the three hypotheses.

The first hypotheses that size selective predation is a major feature in planktivory is strongly supported. In the bluegill, Cladocera of increasing size were taken as the fish grew. When Cladocera of large size were available (*B. longirostris* in May) the larger bluegill took them. When only *B. longirostris* of smaller size were present (July, August) they did not. Larger bodied planktivore species, e.g. *P. pediculus*, were selectively sought, especially when most abundant.

The two small cyprinids, by contrast, took only the smaller zooplankters. They were presumably limited to these by small mouth size and/or ability to handle them. In neither species did the larger individuals take larger zooplankters, possibly because prey size was determined by the size of the favoured *C. sphaericus*. Larger individuals took more chironomids, however, and they were of larger size.

The second hypothesis that small planktivores will consume prey according to abundance levels, and not specialize at the species level, was not supported by the bluntnose minnow and blackchin shiner. It was, however, supported by the smaller bluegill. The first two species fed largely on *C. sphaericus*, which was usually only 1/10 as common as *B. longirostris*. The bluegill, the commonest fish species, by contrast, took mostly *B. longirostris*. This was especially so when this organism was most abundant and of larger size. The killifish, rock bass, and yellow perch, in which planktivory was less predictable, throw no light on the hypothesis.

The third hypothesis that because zooplankton populations fluctuate seasonally no fish species can be exclusively planktivorous is supported. None of the fish were exclusively planktivorous. However, the thesis that planktivorous fish were "forced" to take alternative prey because zooplankton numbers fell so low as not to be able to support them was not supported. Bluntnose minnow and blackchin shiner, the specialist planktivores, obtained ample zooplankton even when prey abundance fell to 1/10. Rather than taking an alternative prey only when zooplankton numbers were lowest they routinely consumed such (Fig. 8). Finally, the chief alternative of all the fish was a single prey type, chironomids.

Prey switching by fish is usually considered to be a response to the simultaneous reduction in abundance of one prey species and increase in another (Murdoch 1969). Experiments carried out by Murdoch failed to support the concept, a finding that he ascribed to the densities of the commonest prey not being high enough, or the experiment being of too short a duration. The existence of a lag time in prey switching is, of course, recognised (Werner et al. 1981). Later work has indicated that prey choice is as much dictated by prey size as abundance (Mittelbach 1981b), with commonly the former being dominant because of energy considerations. Optimum feeding, in turn, is also influenced by such other factors as capacity to capture a particular prey and handling time. (Note here that Werner (1974) found that bluegill took only 1 s to handle a cladoceran but 10 s to handle a smaller chironomid.)

Does the periodic utilization of chironomid larvae as compared with zooplankton by the fish species in this study follow the expectations of prey switching theory? The fact that utilization of noncladoceran prey does not represent a switch but occurs regularly, though at low levels (Fig. 8), suggests that it does not. This would then argue for an alternative explanation that in the bluntnose minnow and blackchin shiner, chironomids, whilst not the major prey, are nevertheless a desired prey type and taken when encountered. Relative to an 0.3- to 0.4-mm *C. sphaericus* with a volume of 0.014–0.021 cm^3, a 5.0-mm chironomid larvae has a body volume of 0.20–0.25 cm^3, 10 times as great. It is hence obviously more energetically rewarding.

How do the findings about planktivore–zooplankter interactions demonstrated here relate to previous work? Firstly, evidence that larger bodied fish concentrate on the larger zooplankters confirms the previous findings of many workers (Hrbáček 1962; Brooks and Dodson 1965; Galbraith 1967; Hall et al. 1970; O'Brien 1979). Lake Opinicon is dominated by the smaller zooplankters. This situation is characteristic of a lake with heavy fish predation (Zaret 1980). It has, moreover, been suggested that the numerical success of *B. longirostris* may be related to fish removing larger competitors (Brooks and Dodson 1965).

There is an anomaly here. Why should fish only remove the larger zooplankters and, specifically, how do *B. longirostris* and *C. sphaericus* maintain good populations in Lake Opinicon in the face of what is obviously high fish predation? There is no obvious answer to this. Zooplankters as a group have a range of adaptations for minimizing fish predation (Drenner et al. 1978; Zaret and Suffern 1976; O'Brien 1979). *Bosmina longirostris* has one additional adaptation not shared by most other zooplankters: summer populations are characterized by small body size and high population turnover rates (Kerfoot 1974).

Specialization on *C. sphaericus* by the two cyprinids and the smaller bluegill on *B. longirostris* was unexpected. Why was the common *B. longirostris* largely avoided by the former fish? Selection of zooplankton prey by fish may be determined by many factors, including abundance, total visibility (Zaret and Kerfoot 1975), and capturability (Zaret 1980). The visibility of zooplankton species may be linked to their shape, amount of body pigmentation, type of motion, and other factors (Eggers 1977; Confer et al. 1978; O'Brien 1979). There are no data available on these factors relative to predation by the Lake Opinicon fishes.

My study provides some new insights into the functioning of planktivore–zooplankter systems. It also highlights the need for further work at the community level.

Acknowledgements

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Effective Solvents and Extraction Periods Employed in Phytoplankton Carotenoid and Chlorophyll Determinations

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Bowles, N. D., H. W. Paerl, and J. Tucker. 1985. Effective solvents and extraction periods employed in phytoplankton carotenoid and chlorophyll determinations. Can. J. Fish. Aquat. Sci. 42: 1127–1131.

Using high-performance liquid chromatography (HPLC), we showed that spectrophotometric determinations of algal lipophilic pigments are often biased by the choice of extraction solvent. Several commonly used extraction solvents and extraction periods were tested on diverse phytoplankton species isolated from the Neuse River, NC. Extraction solvents included 100% acetone, 90% acetone – 10% distilled deionized water (DDW), 50% acetone – 50% methanol, and 90% methanol – 10% DDW. Extraction efficiencies varied significantly among genera. For the diatom *Cyclotella meneghiniana*, at least three solvents extracted all lipophilic pigments with equal efficiency, but 50:50 acetone–methanol was clearly superior for the chlorophycean *Chlorella vulgaris*. A host of differences in extraction efficiencies and extraction times were observed when we compared eukaryotic with prokaryotic (blue-green algae) phytoplankton. We were unable to find a single extraction technique that could consistently provide quantitative and uniform pigment yields from diverse phytoplankton communities. Nevertheless, HPLC techniques can be rapidly and routinely employed to determine appropriate extraction protocols for lipophilic pigments of interest in specific aquatic ecosystems.

À l'aide de la chromatographie en phase liquide à haut rendement, les auteurs ont prouvé que les déterminations spectrophotométriques des pigments lipophiles des algues sont souvent biaisées par le choix du solvant d'extraction. Plusieurs solvants et périodes d'extraction communément employés ont été mis à l'essai sur diverses espèces de phytoplancton isolées des eaux de la rivière Neuse (Caroline du Nord). Les solvants comprenaient : acétone 100 %, acétone 90 % – eau distillée déionisée 10 %, acétone 50 % – méthanol 50 % et méthanol 90 % – eau distillée déionisée 10 %. L'efficacité des extractions a nettement varié d'un genre à l'autre. Chez la diatomée *Cyclotella meneghiniana*, au moins trois solvants ont extrait tous les pigments lipophiles avec la même efficacité; par contre, l'acétone 50 % – méthanol 50 % était nettement supérieur pour la chlorophycée *Chlorella vulgaris*. Une multitude de différences entre les efficacités et les temps d'extraction ont été observées quand on comparait le phytoplancton eucaryote et procaryote (algues bleu-vert). Les auteurs n'ont pas découvert une technique unique d'extraction qui pourrait fournir des rendements en pigment uniformes et quantitatifs à partir de diverses communautés phytoplanctoniques. Toutefois, les techniques de chromatographie en phase liquide à haut rendement peuvent être rapidement et communément employées pour déterminer les méthodes appropriées d'extraction de pigments lipophiles qui présentent un intérêt dans certains écosystèmes aquatiques.

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Spectrophotometric determinations of phytoplankton chlorophyll content were initially developed in the 1930s (Weber et al. 1982). Since then researchers using these methods have introduced numerous modifications to correct for overlapping absorbance spectra and degradation products among diverse pigments characterizing natural phytoplankton communities. Trichromatic formulas published by Richards and Thompson (1952), Parsons and Strickland (1963), and Jeffrey and Humphrey (1975) are attempts to correct for spectral overlaps between chlorophylls *a*, *b*, and *c*. In resolving the problem of absorption spectra interference due to phaeophytin *a* and phaeophorbide *a*, Lorenzen (1967) initiated acidification procedures which alter spectral properties of chlorophyll *a* but not those of breakdown products. However, Rai (1980) noted that such corrections ignore chlorophyllide *a*, and that no method which corrects for breakdown products and accessory pigments, concurrently, is available. As early as 1963, Yentsch and Menzel (1963) were taking advantage of the increased sensitivity and selectivity of fluorescence to distinguish chlorophyll *a* from pheophytin *a* (Yentsch and Menzel 1963; Strickland and Parsons 1972), thus improving analytical pigment determinations.

Despite these analytical improvements, difficulties remain in the quantification of specific chlorophyll and carotenoid pigments from diverse marine (Lorenzen and Jeffrey 1980) and freshwater (Moss 1967) communities. This is not surprising, since a single phytoplankton species may contain as many as 15 distinct chlorophyll and carotenoid pigments as well as their degradation products. Spectral interferences in pigment measurements can be eliminated (rather than corrected for) if pigments are physically separated. Thin-layer chromatography (TLC) is a proven separation method (Jeffrey 1974, 1981; Shiraki et al. 1978; Brown et al. 1982) but it is tedious for routine determinations. Solvent phase separation is another

means of separating pigments (Parsons 1963; Davies 1965). However, solvent miscibility and partial solubility of pigments among diverse solvents pose quantitative problems, hence increasing analytical determination time. High-performance liquid chromatography (HPLC) has distinct advantages over both of these techniques in that quantitative separation, sensitivity, and analytical time are optimized simultaneously. Clarified (filtered and/or centrifuged) extracts are simply injected into the system through which a solvent gradient is pumped for approximately 0.5 h. Solvent gradients are employed to separate virtually all chlorophyll and carotenoid pigments, and a spectrophotometer set at an appropriate wavelength (e.g. 440 nm) can quantitatively detect diverse pigments as they are eluted. Because of its speed, high sensitivity, and effective separation characteristics, HPLC is rapidly becoming a preferred pigment determination technique among limnologists and oceanographers (Stewart and Wheaton 1971; Shoaf 1978; Brown et al. 1981; Grumbach 1983). This method is compatible with traditional pigment extraction techniques. Among extractants, 90% acetone has been favored because quantitative chlorophyll yields are obtained, other lipophilic pigments (chlorophyll degradation products, carotenoids) are effectively (albeit not quantitatively) extracted in parallel, most cellular membranes are rapidly penetrated, and extracts are miscible with a wide variety of organic solvents. The dependence of pigment spectral properties on individual or mixed solvents necessitates the use of different extinction and fluorescence coefficients when using spectrophotometric or fluorometric techniques, respectively. Fortunately, this problem is circumvented when using HPLC with diverse extraction solvents, because once a sample is injected into the system the extraction solvent is swept away by the mobile phase while the absorption (or fluorescence) of each pigment is determined in the same type of eluent each time any sample is processed. HPLC requires no additional sample preparation or alteration following extraction. Simply removing particulate debris from the extract is the only prerequisite for analyses.

In light of the promise of HPLC as a routine pigment determination technique, complimentary knowledge concerning extractants, optimal quantitative yields, and qualitative characteristics of pigments (degradation) is desirable. Accordingly, we examined the compatibility of four widely used extractant mixtures as well as their extraction characteristics over time with HPLC detection of diverse chlorophyll and carotenoid pigments. Choices of extraction times and applicable solvents are important in any pigment measurement. Extraction efficiency for lipophilic pigments is reliant on such factors as phytoplankton type, intracellular pigment location and orientation, pigment affinities for membranes and extraction solvents, solvent–membrane interactions, reactions of solvent and pigment, and most importantly, selectivity for the pigment of interest (Davies 1965; Goodwin 1974). As test solvents we chose 90% (v/v) acetone (routinely used for chlorophyll *a* extraction by physiologists and ecologists), 100% acetone, 90% methanol (often recommended for blue-green algae (Holm-Hansen 1978; Stauffer et al. 1979; Grumbach 1983)), and 1:1 (v/v) acetone–methanol. This study was designed to calibrate and critically examine procedures employing the solvents most commonly used in this laboratory. Other solvents (ethanol, ether, chloroform, and cyclohexane) and combinations with membrane penetrants, such as DMSO and DMF (Stauffer et al. 1979; Burnison 1980), were not tested.

We originally undertook this study to identify optimal solvent extraction techniques coupled to HPLC for quantitative determination of carotenoid and chlorophyll pigments in blue-green algae (Paerl et al. 1983). However, the information obtained proved to be of use for determining extraction characteristics and pigment stability in extracts among diverse phytoplankton taxa hosting a variety of chlorophylls and carotenoids. The information obtained was also relevant to individual pigment analyses.

Methods

Four representative phytoplankton taxa, characterizing the microflora of the eutrophic Neuse River, NC, were isolated under nonaxenic conditions and maintained in exponentially grown batch cultures. Cultures were grown in 2- to 4-L volume Erlenmeyer flasks, fitted with magnetic stirring bars and illuminated by 200 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR). Included were *Microcystis aeruginosa* (Cyanophyceae), *Anabaena oscillarioides* (Cyanophyceae), *Chlorella vulgaris* (Chlorophyceae), and *Cyclotella meneghiniana* (Bacillariophyceae). For each species, 36 subsamples, of equal volume, were withdrawn from a stirred culture, gently vacuum (200 Torr) filtered onto 25-mm-diameter Whatman GF/C filters, rinsed with 2 mL of saturated $MgCO_3$ to prevent acidification, and frozen. Buffered ($MgCO_3$) solutions of 100% acetone, 90:10 (v/v) acetone – distilled deionized water (DDW), 50:50 (v/v) acetone–methanol, and 90:10 (v/v) methanol–DDW were prepared as extracting solvents. All solvents were Fisher HPLC grade.

Each algal type was analyzed individually, since extraction and HPLC analyses lasted 2 d for each experiment. Analytical procedures included sonic disruption, extraction, centrifugation, and HPLC separation. For each solvent, 2 mL was pipetted into nine (three replicates for each extraction time) 15-mL Nalgene (LPE) centrifuge tubes into which frozen filters were placed and sonicated for 30 s. The tubes were then covered and returned to the freezer (−20°C) for extraction periods of 1, 6, and 24 h. At the end of each extraction period we removed three replicates for each solvent and centrifuged them for 5 min at 2800 rpm. The supernatant was recentrifuged to thoroughly eliminate fine particles.

Spectral scans and HPLC analyses were performed on the supernatant. We scanned a 1:1 dilution of the supernatant with representative solvents from 850 to 350 nm, using a Bausch & Lomb Spectronic 2000 double beam spectrophotometer. Next, a 20-μL undiluted extract sample was injected into a Altex model 110 high-performance liquid chromatograph equipped with a 25-cm-long ultrasphere ODS-18 reverse phase column and a Hitachi 100-10 spectrophotometric detector having an 8-μL volume microflow-cell. Chromatographs were plotted on a Hewlett Packard 3390A integrating recorder. The mobile phase, a gradient of solvents A (90:10 (v/v) methanol–acetonitrile) and B (100% acetone), was regulated according to the following program: 0–7 min 100% A, 7–11 min linear increase to 60% B, 11–20 min 60% B, 20–28 min linear decrease to 100% A. The flow rate was 1.5 $mL \cdot min^{-1}$. A representative chromatograph is shown in Fig. 1. All mobile phase chemicals were Fisher HPLC grade. Paerl et al. (1983) developed this program to separate the lipophilic pigments of blue-green algae. Complete separation of the pigments of other algal groups may require modifications to the program (Eskins et al. 1977; Braumann et al. 1978; Braumann and Grimme 1979). Other

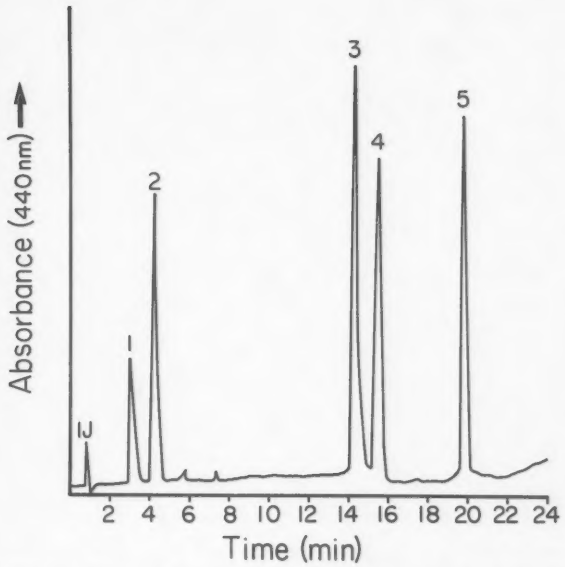

FIG. 1. Representative chromatograph of lipophilic pigments obtained from the blue-green alga *M. aeruginosa* using our solvent gradient program. Quantifiable pigments observed in this organism included (1) myxoxanthophyll, (2) zeaxanthin, (3) chlorophyll *a*, (4) echinenone, and (5) β-carotene.

programs are used to quickly (10 min) analyze chlorophylls and their breakdown products (Brown et al. 1981).

The dominant lipophilic pigments of the blue-green algae *A. oscillarioides* and *M. aeruginosa* have previously been identified by Paerl et al. (1983) using this technique. Pigments identified included chlorophyll *a*, myxoxanthophyll, zeaxanthin, echinenone, and β-carotene. In the current study, chlorophylls *b* and *c* were also identified. Chlorophyll *c* was identified by comparing HPLC analyses of a concentrated sample of the diatom *Cyclotella meneghiniana* at 440 nm and at 630 nm (an absorption maximum for chlorophyll *c* not readily absorbed by chlorophyll *a* or carotenoid pigments). Carotenoid pigments of *Cyclotella meneghiniana* and *Chlorella vulgaris* were initially separated on a MgO column (Strain and Sherma 1972) and reconcentrated by the evaporation of excess solvent. These concentrated samples were initially analyzed by TLC (Jeffrey 1981) for identification and subsequently examined by HPLC for elution times. In this manner the lipophyllic pigments of *Anabaena*, *Microcystis*, *Cyclotella*, and *Chlorella* were identified as shown in Fig. 1. Pigment identification by TLC and HPLC was facilitated by chlorophyll *a*, chlorophyll *b*, and β-carotene standards obtained from the Sigma Chemical Company and echininone and zeaxanthin standards kindly donated by Hoffman-La Roche, Switzerland. Additional confirmative evidence was obtained by comparing TLC-derived R_f values for relevant pigments with previously published results (Stransky and Hager 1970; Jeffrey 1981; Paerl 1984).

Results

Chlorophylls *a*, *b*, and *c* and major carotenoid pigments representative of the phytoplankton taxa examined were all detectable at 440 nm by HPLC without necessitating concentration prior to sample injection. Among the two blue-green algae,

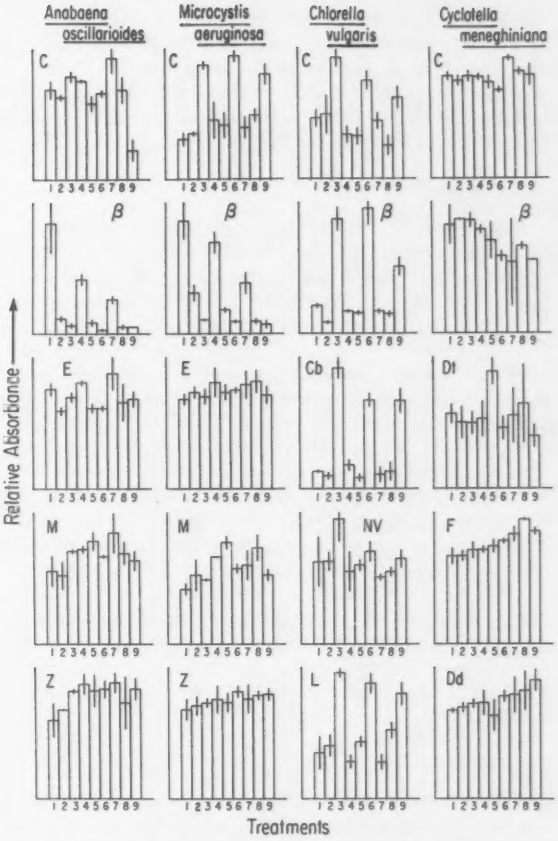

FIG. 2. Comparisons of treatments (1–9) for each major pigment of the four algal genera. Treatments: (1) 100% acetone for 1 h, (2) 90%–10% acetone–DDW for 1 h, (3) 50%–50% acetone–methanol for 1 h, (4) 100% acetone for 6 h, (5) 90% acetone for 6 h, (6) acetone–methanol for 6 h, (7) 100% acetone for 24 h, (8) 90% acetone for 24 h, (9) acetone–methanol for 24 h. Pigments: C, chlorophyll *a*; β,β-carotene; E, echininone; M, myxoxanthophyll; Z, zeaxanthin; Cb, chlorophyll *b*; NV, neoxanthin/violaxanthin; L, lutein; F, fucoxanthin; Dd, diadioxanthin; Dt, diatoxanthin.

chlorophyll *a*, myxoxanthophyll, zeaxanthin, echinenone, and β-carotene were consistently identified and quantifiable. *Cyclotella meneghiniana* characteristically contained chlorophylls *a* and *c* as well as diadinoxanthin, diatoxanthin, fucoxanthin, and β-carotene, while chlorophylls *a*, and *b*, violaxanthin, neoxanthin, lutein, and β-carotene were the major pigments of *Chlorella vulgaris* (Fig. 2).

Of the extraction solvents tested, 90% methanol proved to be least effective among all algal groups. Numerous methanol extractions yielded samples below the level of analytical detection. The results consistently indicated that pigment (both chlorophylls and carotenoids) degradation during extraction periods led to poor recovery and detectability among pigments of interest when this extractant was used. Since several researchers have reported methanol to be an efficient extractant of chlorophyll *a* (Holm-Hansen 1978; Stauffer et al. 1979; Grumbach 1983), we performed an additional test using absolute methanol. We found no difference between the two concentrations of methanol. Wood (1985) suggests a 1:1 mixture of

chloroform–methanol for chlorophyll *a* extraction but the stability of carotenoids in this solvent remains unknown. Methanol extractions were excluded from all subsequent statistical analyses except for an initial *t*-test which showed it to be significantly ($P < 0.001$) inferior to the most effective extractant for at least two major pigments in each species tested.

Chlorophyll *a*

Responses to extractants and extraction times varied between species and among individual pigments within a single species. For examining chlorophyll *a* the choice of a specific solvent was less critical among *Cyclotella* and *Chlorella* than among either blue-green algae tested. Overall, chlorophyll *a* was most effectively extracted from all four species by 1:1 (v/v) acetone–methanol for 1–6 h, with 100% acetone being the best alternative solvent. The two concentrations of acetone (100 and 90%) tested showed increased extraction over time, with optimal extraction occurring at 24 h. Optimal extraction efficiencies were reported at 1 h when acetone–methanol served as the extractant; longer extraction periods led to slight but consistent decreases in pigment yields (for chlorophylls and carotenoids). Acetone–methanol proved to be the most effective and stable extractant over the entire extraction period for *Chlorella* and *Microcystis*. It was also the best chlorophyll *a* extractant for all species tested at 1 h. An analysis of variance indicated that chlorophyll *a* extraction strongly relied on solvent characteristics in all four species. In addition, chlorophyll *a* extraction was time dependent in the two eukaryotic species, *Cyclotella* and *Chlorella*.

β-Carotene

β-Carotene commonly occurred in all species examined. Its degradation was time dependent in all species. One hour was clearly the optimal extraction time for this pigment. Possibly, shorter extraction times may have proven superior; however, they were not attempted in this study, since pigment extractions routinely deployed for limnological and oceanographic purposes are generally not conducted and analyzed within 1 h. In considering solvent extraction characteristics for β-carotene, contrasts were obtained among diverse species. In *Cyclotella*, all solvents (excluding 90% methanol) gave similar β-carotene yields. However, among the remaining species, solvent choice proved critical. Acetone–methanol was the preferred extractant for *Chlorella*, while 100% acetone was the optimal extractant for both blue-green algae. Significant differences in β-carotene extraction efficiencies, observed between 90 and 100% acetone extractions among the blue-green algae, were not found in the eukaryotes tested.

Discussion

Because of marked differences in optimal extractants for the dominant lipophilic pigments chlorophyll *a* and β-carotene (Fig. 3) within a single species, the choice of a universal extractant applicable to the entire suite of lipophilic pigments of interest is difficult. To illustrate this problem, among the blue-green algae examined, major xanthophylls, chlorophyll *a*, and β-carotene were optimally extracted by different solvents. In the case of xanthophylls, acetone–methanol proved best, while chlorophyll *a* was optimally extracted by 90% acetone and β-carotene was most effectively extracted by 100% acetone. To add to this dilemma, contrasting extraction times selectively

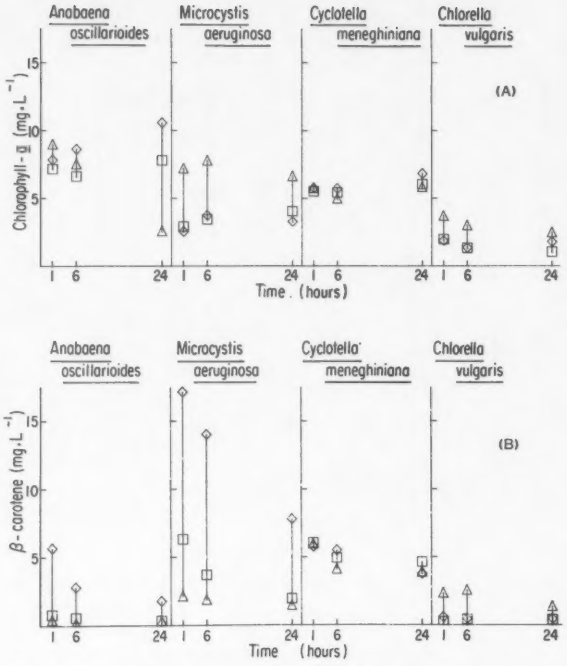

FIG. 3. Comparative (a) chlorophyll *a* and (b) β-carotene extraction efficiencies for three commonly used solvents tested on four representative genera characterizing the phytoplankton community of the Neuse River, NC. Solvents: ◇, 100% acetone; □, 90% acetone – 10% distilled deionized water; △, 50% acetone – 50% methanol. Vertical lines reveal the magnitudes of extraction differences among these solvents.

favor the quantitative yield of one pigment over the other. Since the choice of solvent and extraction time is most critical for effective β-carotene yields, we recommend a 100% acetone extraction for 1 h as a general solvent for blue-green algae. In contrast, for *Cyclotella*, solvent choice is relatively unimportant (except for 90% methanol, which was generally ineffective), but extraction time should be confined to 1 h to minimize β-carotene degradation. If we additionally consider *Chlorella*, acetone–methanol is a superior extractant, with 1 h being an optimal extraction period.

If quantitative extraction of β-carotene is not necessary, acetone–methanol becomes the most useful and universal extractant for the blue-green algae examined. If one wishes to specifically examine blue-green algal xanthophylls, 90% acetone extractions for 6 h are preferred. Either of these choices will also effectively extract and preserve chlorophyll *a*. Hence, we conclude that for general use, acetone–methanol or 90% acetone is the preferred solvent for either trichromatic spectrophotometric or chromatographic analyses of lipophilic pigments in prokaryotic and eukaryotic phytoplankton.

We have presented HPLC analyses based on diverse phytoplankton taxa. The results obtained thus far emphasize the need to tailor extractants and extraction times to particular conditions of phytoplankton community composition as well as pigments of interest. Although it is difficult to prescribe a universal extractant and extraction time suitable to all natural phytoplankton assemblages, it is possible to utilize appropriate methods for maximizing extraction efficiencies when knowledge of species

dominance is available. Furthermore, when encountering nearly unialgal blooms or examining specific laboratory populations, quantitative extractions of pigments of interest can be obtained when following methodological protocols prescribed in this study.

Acknowledgments

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The Influence of Fish–Zooplankton–Phytoplankton Interactions on the Results of Selenium Toxicity Experiments Within Large Enclosures

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Salki, A., M. Turner, K. Patalas, J. Rudd, and D. Findlay. 1985. The influence of fish–zooplankton–phytoplankton interactions on the results of selenium toxicity experiments within large enclosures. Can. J. Fish. Aquat. Sci. 42: 1132–1143.

The response of zooplankton to sodium selenite at concentrations of 1, 10, and 100 μg $Se \cdot L^{-1}$ was studied using large (100 m^3) enclosures in mercury-contaminated Clay Lake, Ontario (50°03′N, 90°30′W). Crustacean community development in treated enclosures exhibited no obvious acute or chronic effects from the range of selenium concentrations applied. Seasonal changes in zooplankton composition, abundance, and reproduction were similar among controls and the 1 and 10 μg $Se \cdot L^{-1}$ enclosures. Differences in species dynamics observed in the 100 μg $Se \cdot L^{-1}$ enclosure and in a sediment control enclosure were attributable to biotic interactions rather than selenium. Predation appeared to be the dominant factor governing zooplankton community structure in all enclosures. Differences in the number of planktivorous fish among enclosures led to variations in the abundance of predatory *Leptodora kindtii*, which in turn affected abundances of the small cladoceran *Bosmina longirostris*.

La réaction du zooplancton à des concentrations de sélénite de soude de 1, 10 et 100 μg $\cdot L^{-1}$ a été étudiée dans de grands enclos (100 m^3) situés dans le lac Clay (50°03′N, 90°30′O), en Ontario, qui est contaminé par le mercure. Le développement des communautés de crustacés dans les enclos traités n'a pas montré d'incidence chronique ou aiguë apparente aux différentes concentrations de sélénium appliquées. Les variations saisonnières de la composition, de l'abondance et de la reproduction des communautés zooplanctoniques étaient semblables pour les enclos témoins et les enclos traités à 1 et 10 μg $\cdot L^{-1}$. Les différences pour la dynamique des espèces observées entre l'enclos traité à 100 μg $\cdot L^{-1}$ et un enclos témoin des sédiments sont attribuables à des interactions biotiques et non au sélénium. La prédation semblait être le facteur dominant qui régissait la structure des communautés zooplanctoniques dans tous les enclos. Les différences entre le nombre de poissons planctivores de chaque enclos ont mené à des variations de l'abondance du prédateur *Leptodora kindtii*, ce qui a influé sur le nombre du petit cladocère *Bosmina longirostris*.

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Contamination of the English–Wabigoon River system with mercury from industrial discharges near Dryden, Ontario, resulted in some of the highest mercury concentrations in aquatic biota ever reported (Armstrong and Hamilton 1973; Jackson et al. 1980). The addition of selenium was suggested as a possible method to reduce mercury bioaccumulation in this waterway (Rudd et al. 1980; Rudd et al. 1983; Turner and Rudd 1983). Selenium can reduce mercury toxicity (Parizek and Ostadalova 1967; Ganther et al. 1972; Potter and Matrone 1974), but its overall impact on aquatic ecosystems is not fully understood. Although acute toxicity thresholds for selenium have been determined in vitro for several species of zooplankton (Halter et al. 1980; Schultz et al. 1980), these levels cannot be simply extrapolated to the natural environment because of the interaction of species with other biotic and abiotic components (Levin 1982). Large-scale enclosures offer advantages over in vitro bioassays for examining such interactions (Menzel and Steele 1978; Grice et al. 1977).

In 1978 and 1979, several 10-m-diameter enclosures were placed in mercury-contaminated Clay Lake, Ontario (50°03′N, 90°30′W), to investigate the efficacy of selenium as an agent for ameliorating mercury toxicity and to determine the ecological effects of selenium. Initial results indicated that selenium accumulated in all components of the foodweb. Mercury bioaccumulations were reduced in organisms higher in the food web (fish, crayfish, phantom midges) but not in lower ones (clams, snails, plankton) in enclosures treated with selenium (Turner and Rudd 1983). The primary objective of the present experiment was to examine the response of zooplankton to selenium concentrations of 1, 10, and 100 μg $Se \cdot L^{-1}$. In addition, the use of large-scale enclosures permitted the assessment of biotic interactions which could influence the outcome of the selenium toxicity experiment.

Materials and Methods

Five polyethylene-walled experimental enclosures were set into a sheltered bay in the eastern basin of Clay Lake on July 10, 1979. Each 10-m-diameter mesocosm (wall area = 52 m^2) enclosed about 79 m^2 of sediment and 130 m^3 of water (Turner

TABLE 1. Summary of transparency and selected features of water chemistry in the experimental enclosures (data reported as seasonal means ± SD).

Analysis	No. of observations	Enclosure C_1	Enclosure C_2	Enclosure C_x	S_1 (1 μg Se·L^{-1})	S_{10} (10 μg Se·L^{-1})	S_{100} (100 μg Se·L^{-1})
Total C (mmol·L^{-1})	2	2.13 (±0.15)	2.05 (±0.08)	1.96 (±0.02)	2.03 (±0.01)	2.05 (±0.11)	2.00 (±0.12)
Total N (μmol·L^{-1})	3	55 (±7)	48 (±8)	46 (±6)	52 (±7)	45 (±3)	56 (±16)
Total P (μmol·L^{-1})	3	2.5 (±0.7)	2.0 (±0.2)	1.4 (±0.2)	2.1 (±0.3)	2.2 (±0.3)	2.1 (±0.0)
Chlorophyll (μg·L^{-1})	7	11.1 (±4.2)	8.5 (±1.8)	11.0 (±4.8)[a]	10.0 (±6.0)	8.6 (±2.8)	17.2 (±13.7)
pH	3	7.82 (±0.07)	7.68 (±0.08)	7.79 (±0.04)	7.73 (±0.06)	7.64 (±0.06)	8.14 (±0.63)
Secchi depth (m)	20	0.94 (±0.17)	1.12 (±0.18)	0.96 (±0.17)	0.99 (±0.19)	0.97 (±0.16)	0.91 (±0.15)

and Rudd 1983). Approximately 0.10 GBq of $H_2{}^{75}SeO_3$ (New England Nuclear Corp.) with a trace amount of carrier selenium was added to each of the five enclosures on July 16. Sufficient sodium selenite was added with the ^{75}Se to three enclosures to yield initial nominal concentrations of 1, 10, or 100 μg Se·L^{-1} (S_1, S_{10}, and S_{100}, respectively). Two control enclosures (C_1, C_2) received no other chemical additions. By late August, ambient selenium concentrations in the treatment enclosures had declined to approximately one-half initial levels. Concentrations of stable selenium isotopes in water of the control enclosures were below the analytical detection limit of 0.2 μg Se·L^{-1}.

On July 11, 1979, a sixth mesocosm (C_x-sediment feedback control) was installed over an area of sediment enclosed during 1978 by a similar enclosure. The 1978 enclosure had been used as a control for mercury experiments (Rudd et al. 1983). Rotenone was added to this enclosure (≈8 mg·L^{-1}) in the fall of 1978. Subsequently, the enclosure froze into the winter ice and was then removed in the spring of 1979. The sediment remained exposed to lake circulation for approximately 1.5 mo before installation of a new polyethylene wall, the beginning of C_x. Although the wall area of C_x was similar, sediment area and water volume were about 80% of the other mesocosms because the wall was sealed into the sediments within the perimeter of the previous enclosure. Enclosure C_x did not receive any chemical or further radiochemical additions.

Fish unintentionally trapped during enclosure implacement were removed using minnow traps and gill nets prior to any chemical additions. On July 17, 70 adult pearl dace (*Semotilus margarita*), collected from a nearby lake uncontaminated by mercury, were added to each enclosure (≈48 kg·ha^{-1}). Most of the dace escaped from C_x within a week of their addition due to an incomplete seal of the polyethylene wall to the sediments. The temporary water exchange between the lake and enclosure C_x was estimated to be no greater than 20% on the basis of sodium ion loss from the enclosure (Rudd et al. 1980). Thirteen young-of-the-year yellow perch (*Perca flavescens*) were also added (≈1.5 kg·ha^{-1}) to each mesocosm on July 19. As part of a concurrent research project (Turner and Rudd 1983; Turner and Swick 1983), pearl dace and yellow perch were removed periodically from all enclosures. Following addition of rotenone to the mesocosms at the end of the experiment it became apparent that not all fish had been removed by the initial netting procedure prior to stocking of the pearl dace and yellow perch. Based on the experimental stocking and removal of fish, the following biomass was estimated to exist at the start of the experiment in enclosures C_1, C_2, C_x, S_1, S_{10}, and S_{100}, respectively: young-of-the-year yellow perch 5.1, 1.3, 1.5, 6.1, 9.6, and 0.8 kg·ha^{-1}, and young white sucker (*Catostomus commersoni*) 4.9, 4.4, 3.5, 10.3, 3.9, and 0.9 kg·ha^{-1}. These values were determined from yellow perch estimated to weigh 1 mg each initially. In addition, initial biomass of white sucker was assumed to be one-half of final biomass resulting from growth during the experiment, approximately in parallel with observed rates of growth by yellow perch (Turner and Rudd 1983). The corresponding initial total numbers of fish in enclosures C_1, C_2, C_x, S_1, S_{10}, and S_{100} were 57, 23, 20, 112, 147, and 13, respectively.

Water chemistry was determined using the methods of Stainton et al. (1977). Total and methyl mercury concentrations in water were similar in all enclosures (Turner and Rudd 1983). Seasonal mean values of total carbon, nitrogen, or phosphorus yielded no differences (Table 1).

Bioaccumulation of stable selenium by net plankton was estimated from ^{75}Se uptake (Hesslein et al. 1980; Turner and Rudd 1983). The amount of selenium bioaccumulated by net plankton (>73 μm) was a function of the ambient selenium concentration, with maximum concentrations in biota being achieved later at higher selenium concentrations (refer to Turner and Rudd 1983).

Carbon-14 incubator assays of phytoplankton primary productivity were performed biweekly using the methods of Fee (1973) and Shearer (1976a, 1976b). Chlorophyll *a* and phytoplankton samples were taken weekly using a rigid PVC tube which sampled all depths within the enclosures uniformly. Chlorophyll *a* was determined from the procedure of Stainton et al. (1977). Mean chlorophyll *a*, pH, and Secchi values were comparable among enclosures with the exception of the S_{100} enclosure which exhibited higher chlorophyll *a* and pH levels and enclosure C_2 which gave greater Secchi readings. In S_{100}, higher algal primary production was observed in association with the higher chlorophyll *a* concentrations (Fig. 1). In C_2,

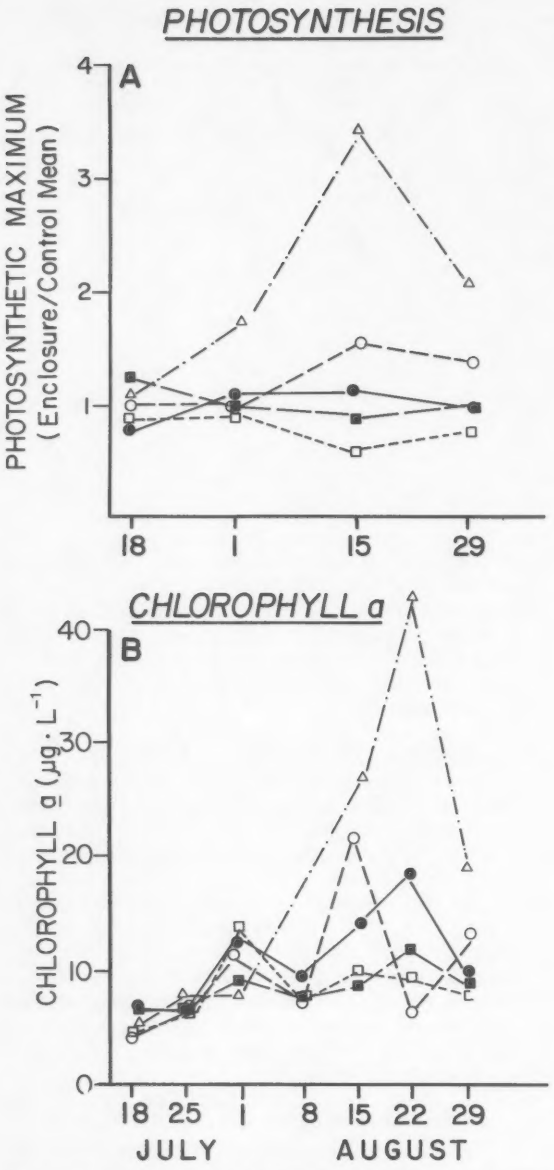

FIG. 1. Changes in (A) phytoplankton–photosynthesis and (B) chlorophyll *a* concentrations in control (C_1, ●; C_2, ■) and treatment (S_1, ○; S_{10}, □; S_{100}, △) enclosures, July 18 – August 27, 1979. On each sampling day, the maximum photosynthetic rate observed in the incubator for an enclosure was expressed as a fraction of the mean of the controls (Turner and Rudd 1983).

water transparencies were consistently 0.1–0.2 m greater than in other enclosures. Lake transparencies, on the other hand, were always 0.2–0.5 m less than enclosure values.

Unconcentrated phytoplankton samples (40 mL) were preserved with 1 mL of acid Lugol solution, and about 1 mo later, 2 mL of 100% formalin was added. A 10-mL aliquot, allowed to settle for 24 h, was analyzed using an inverted microscope (125–400×) and the Utermohl technique as modified by Nauwerck (1963). Algal biomass was calculated from cell dimensions and formulae of the closest fitting geometric shape (Vollenweider 1968).

Zooplankton samples for taxonomic analysis were collected weekly during the midsummer season July 18 – August 27, 1979, from the enclosures and adjacent waters of Clay Lake. Within each enclosure, total vertical samples were taken with a modified Pennak tube (Salki 1981) from 11 stations distributed along two perpendicular diameters. All 11 samples were combined (60 L in total) and filtered through a 73-μm-mesh net. An equivalent volume was collected from random sites adjacent to the enclosures, hereafter referred to as the "lake." Zooplankton were initially narcotized in 5% ethanol (Gannon and Gannon 1975) and then preserved in 5% formalin. Similarly, a second set of samples for radioassay of ^{75}Se was collected from each enclosure (except C_x), filtered through preweighed filters (GFC), and dried at 60°C (Turner and Rudd 1983).

Reproducibility of sampling with the flexible tube was confirmed in control C_1 on August 7 when little variation in dry weight biomass between duplicate samples (coefficient of variation, cv = 6.3%) was found. Duplicate samples for taxonomic analysis collected from the lake on July 25 and 30 also showed low variability of total crustacean abundance, cv = 9 and 10%, respectively.

An instar analysis was applied to plankton samples because sensitivity to contaminants is a direct function of the size or stage of an organism (Reeve et al. 1977). All instars, except for calanoid and cyclopoid nauplii, were identified to species according to Yeatman (1959), Wilson (1959), and Brooks (1957). Zooplankton abundance, reported as individuals per litre, was estimated from pipetted subsamples of between 2 and 10% with a minimum of 200 individuals counted (Cassie 1971). Abundances of *Leptodora kindtii*, *Chaoborus* sp., and other large, less common species were determined from examination of the entire sample. Zooplankton biomass (micrograms wet weight per litre) was estimated from measurements of individual species and the length–weight relationships of Klekowski and Shushkina (1966) and Pechen (1965) (cited in Edmondson 1971). Estimates of fecundity were obtained from 10 to 20 gravid females selected randomly from each sample.

The acute toxicity of selenium to the zooplankton community was assessed by examining the similarity in species composition between control and treatment enclosures. The percentage similarity between a pair of samples was obtained by summing the smaller percentage abundance value for each species pair (Raabe 1952; Southwood 1968, p. 333). The similarity was 100% if the relative proportion of each species in the two systems was identical and 0% if there were no species in common. Acute effects at the species level were examined by comparing the abundances of mature and immature instars among initial samples.

Effects of chronic exposure to selenium were evaluated from seasonal changes in similarity between control and treatment communities. Based on Smith et al. (1982), changes greater than 25% were considered to signify a response to either a treatment or some environmental factor.

Differences in the fecundity of *Tropocyclops prasinus mexicanus* and *Bosmina longirostris* between control and treatment enclosures were detected using a one-way ANOVA. They were used as an indication of chronic, sublethal toxicant stress (Reeve et al. 1977).

TABLE 2. Phytoplankton community composition and biomass within experimental enclosures (except C_x) at the start (July 17) and end (August 29) of the study.

	No. of species identified		Total biomass ($\mu g \cdot L^{-1}$)		% composition							
					Chrysophytes		Chlorophytes		Cryptophytes		Cyanophytes	
Enclosure	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
C_1	31	17	472	413	63.2	3.3	8.7	60.2	10.2	31.6	0.1	0.0
C_2	38	18	482	260	38.7	6.2	10.9	42.0	10.1	48.2	1.8	0.6
S_1	30	17	297	374	58.1	1.7	11.3	77.8	5.8	17.9	1.7	1.2
S_{10}	31	17	580	621	48.5	56.4	6.5	15.2	11.5	20.8	0.1	0.1
S_{100}	34	20	728	4813	52.5	3.2	6.7	1.7	14.0	1.4	0.1	83.5

Results

Phytoplankton

Algal species composition was relatively similar with 30–38 species identified in each enclosure (Table 2). Chrysophytes initially dominated all algal communities. In late August, total phytoplankton biomass ranged from 260 to 620 $mg \cdot m^{-3}$ among enclosures C_1, C_2, S_1, and S_{10} but reached 4800 $mg \cdot m^{-3}$ in S_{100}. Cyanophytes constituted most of the large accumulation in S_{100}, while chlorophytes formed a large proportion of final biomass in enclosures C_1, C_2, and S_1. In S_{10}, chrysophytes were the major algal group in late August.

Zooplankton

Acute effects

Eight days after enclosure installation and 2 d following selenium addition, similar crustacean communities were found in all enclosures (Fig. 2A). Zooplankton were distributed randomly ($P > 0.05$) with total abundances ranging from 29.2 to 50.8 $ind \cdot L^{-1}$ (cv = 21%) among enclosures. Slightly lower levels, 17.9 $ind \cdot L^{-1}$, existed in the lake. Initial community biomass, excluding *L. kindtii*, was relatively constant, from 0.12 to 0.20 mg wet weight $\cdot L^{-1}$ (cv = 20%) among enclosures and 0.12 mg wet weight $\cdot L^{-1}$ in the lake (Fig. 2B). Relatively high (75–92%) percentage similarities were noted between communities in the enclosures (Table 3) due mainly to the predominance of *T. p. mexicanus*.

On the first sampling occasion nine species were common to all enclosures and the lake and represented between 95.5 and 100% of community abundance (Fig. 3). Numerically, these species were similar among enclosures. The major cyclopoid, *T. p. mexicanus*, ranged from 19.4 to 39.6 $ind \cdot L^{-1}$ (cv = 22%). Although *Acanthocyclops vernalis* was less abundant, from 3.4 to 7.7 $ind \cdot L^{-1}$, this species was distributed uniformly among enclosures (cv = 29%). *Diaptomus oregonensis* abundance was similar among enclosures and the lake. Cladocerans, the most diverse group with 12 species identified, were not abundant initially with 1.2–4.2 $ind \cdot L^{-1}$ in the enclosures. Highest abundances of *Daphnia galeata mendotae* and *L. kindtii* but lowest abundances of *B. longirostris* occurred in enclosures C_x and S_{100}.

The instar analysis of all cyclopoid and calanoid species as well as *Daphnia retrocurva* and *D. g. mendotae* revealed similar proportions of immature and mature individuals in all enclosures 2 d after selenium addition (Fig. 3).

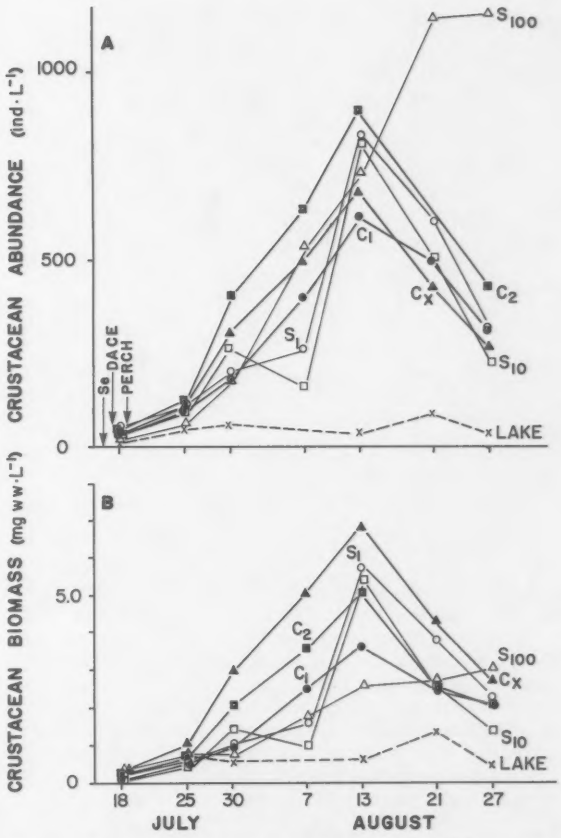

FIG. 2. Changes in (A) crustacean abundance and (B) biomass in control (C_1, ●; C_2, ■), treatment (S_1, ○; S_{10}, □; S_{100}, △), and sediment feedback (C_x, ▲) enclosures and in Clay Lake (×), July 18 – August 27, 1979.

Chronic effects

Through the course of the experiment, changes in total abundance and biomass were similar among enclosures (Fig. 2). Abundances peaked in mid-August between 603 and 903 $ind \cdot L^{-1}$ (cv = 15%), except in S_{100} where crustaceans increased steadily to 1153 $ind \cdot L^{-1}$ on August 27. Total biomass followed similar trends although values in C_x were relatively higher. Seasonal mean abundances and biomass were similar among

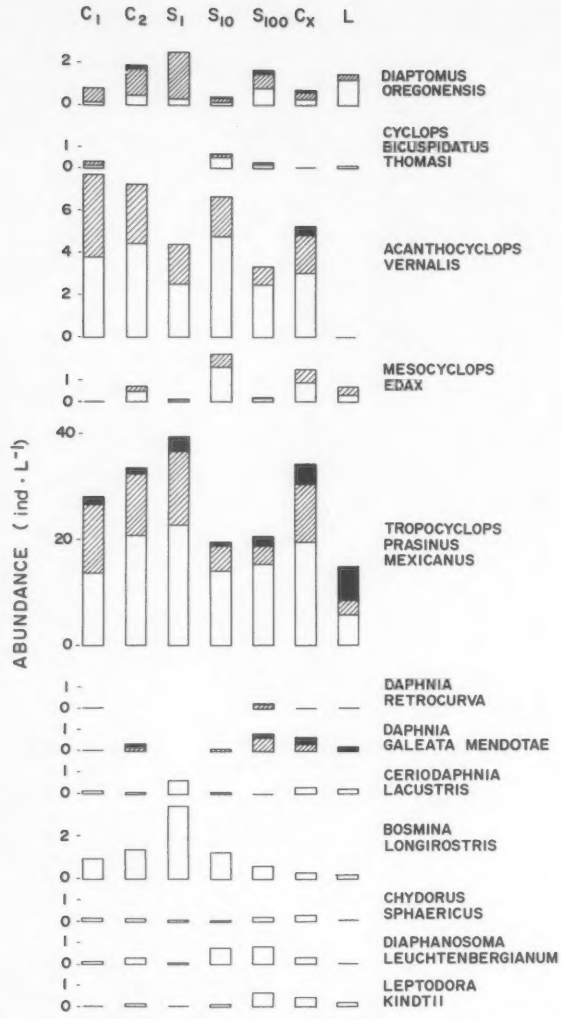

FIG. 3. Abundance of major zooplankton species in control (C_1, C_2), treatment (S_1, S_{10}, S_{100}), and sediment feedback (C_x) enclosures and Clay Lake (L) on July 18, 2 d after selenium addition. Cyclopoid and calanoid species abundance histograms are divided into nauplius (clear), copepodid I–V (hatched), and adult (shaded) portions. Daphnid species are divided into immature (hatched) and mature (shaded) fractions.

enclosures (cv = 15 and 14%, respectively) except for the higher abundance in S_{100} and higher biomass in C_x (Fig. 4). The lake mean abundance and biomass were only 13 and 28% of respective mean values of control enclosures.

No seasonal change in community composition was observed with the nine common species persisting throughout the observation period. This group comprised almost 100% of mean total abundance in each enclosure except C_x and the lake, which had respective values of 90.8 and 94.8%. Six moderate to large species, *D. oregonensis*, *Acanthocyclops vernalis*, *Mesocyclops edax*, *L. kindtii*, *Diaphanosoma leuchtenbergianum*, and *Ceriodaphnia lacustris* were from 3.3 to 7.5 times more abundant in C_x than in other enclosures (Fig. 4). Also, two large cladocerans, *D. retrocurva* and *D. g. mendotae* were, respec-

TABLE 3. Percent similarities (Raabe 1952) among enclosure and lake crustacean community pairs on July 18, 2 d after selenium addition.

	C_2	S_1	S_2	S_3	C_x	Lake
C_1	92.1	85.1	86.7	88.7	84.7	76.1
C_2		89.7	84.0	90.1	91.1	81.3
S_1			75.4	86.3	89.8	85.5
S_2				80.2	79.9	68.8
S_3					88.0	80.8
C_x						86.5

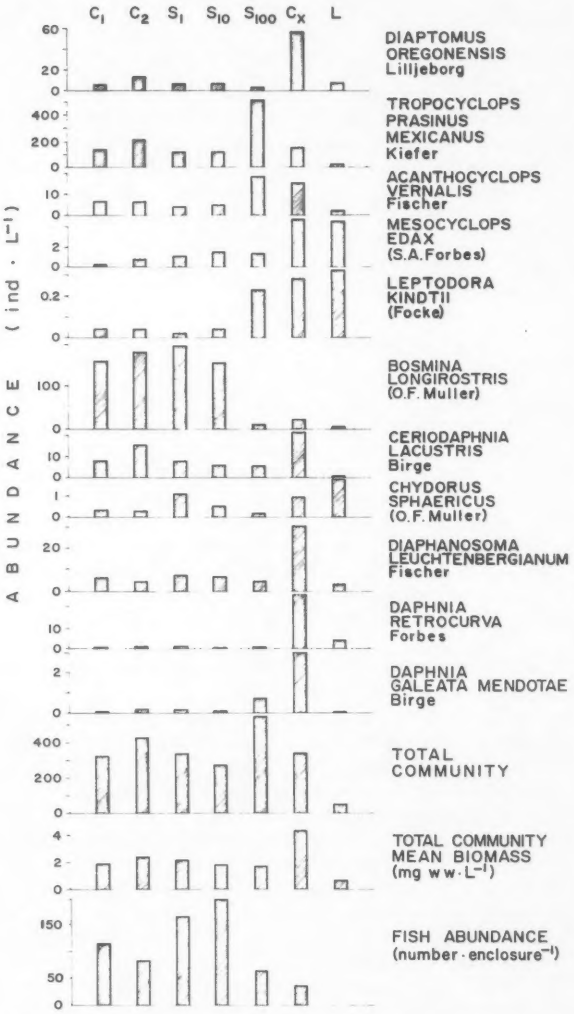
C1 C2 S1 S10 S100 Cx L
DIAPTOMUS OREGONENSIS Lilljeborg
TROPOCYCLOPS PRASINUS MEXICANUS Kiefer
ACANTHOCYCLOPS VERNALIS Fischer
MESOCYCLOPS EDAX (S.A. Forbes)
LEPTODORA KINDTII (Focke)
BOSMINA LONGIROSTRIS (O.F. Muller)
CERIODAPHNIA LACUSTRIS Birge
CHYDORUS SPHAERICUS (O.F. Muller)
DIAPHANOSOMA LEUCHTENBERGIANUM Fischer
DAPHNIA RETROCURVA Forbes
DAPHNIA GALEATA MENDOTAE Birge
TOTAL COMMUNITY
TOTAL COMMUNITY MEAN BIOMASS (mg ww · L⁻¹)
FISH ABUNDANCE (number · enclosure⁻¹)
ABUNDANCE (ind · L⁻¹)

FIG. 4. Mean community abundance and biomass and mean abundance of predominant crustacean species in control (C_1, C_2), treatment (S_1, S_{10}, and S_{100}), and sediment feedback (C_x) enclosures and Clay Lake (L), July 18 – August 27, 1979. Mean total numbers of yellow perch, white sucker, and pearl dace in the six enclosures during the same period are also included.

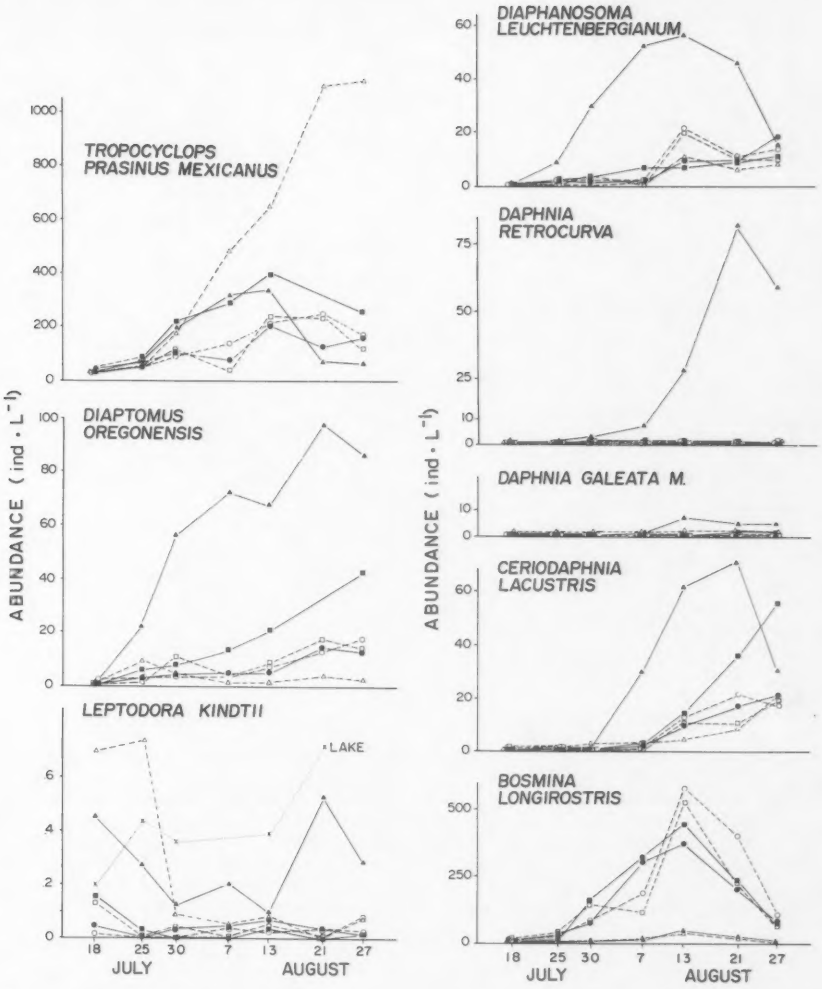

FIG. 5. Changes in the abundance of *T. p. mexicanus*, *D. oregonensis*, *L. kindtii*, *D. leuchtenbergianum*, *D. retrocurva*, *D. g. mendotae*, *C. lacustris*, and *B. longirostris* in control (C_1, ●; C_2, ■), treatment (S_1, ○; S_{10}, □; S_{100}, △), and sediment feedback (C_x, ▲) enclosures, July 18 – August 27, 1979. Abundance of *L. kindtii* in Clay Lake is also shown (×).

tively, 116 and 15 times more numerous in C_x than in the other enclosures. However, in C_x the smaller cladoceran *B. logirostris* attained only 13% of values in C_1, C_2, S_1, and S_{10}. Similar low abundances of *B. longirostris* occurred also in S_{100} and the lake. High abundances (mean = 501 ind·L^{-1}) of *T. p. mexicanus* were observed in enclosure S_{100}.

The temporal changes in development of each species provided the clearest indication of the similarities and differences among enclosures (Fig. 5). The abundance of *T. p. mexicanus* rose continuously until mid-August in all enclosures; in addition, S_{100} increases persisted into late August due mainly to nauplii. Increases of *D. oregonensis* were comparable in enclosures C_1, S_1, S_{10}, and S_{100}, but in C_x, numbers were 4 times higher by late August. *Diaphanosoma leuchtenbergianum*, *D. retrocurva*, *D. g. mendotae*, and *C. lacustris* all attained much higher abundances in C_x than in other enclosures. Changes in *B. longirostris* were very similar in C_1, C_2, S_1, and S_{10} all with mid-August peaks near 400–500 ind·L^{-1}, but in C_x and S_{100}, August maxima were only 94 and 39 ind·L^{-1}, respectively. The dynamics of these species in the lake were similar to those in the enclosures but abundances were considerably lower. *Leptodora kindtii* abundances were consistently below 0.1 ind·L^{-1} in C_1, C_2, S_1, and S_{10} but were much higher in C_x throughout the study. In S_{100}, *Leptodora* was particularly abundant on the first two sampling occasions. Although it subsequently declined, it remained consistently above levels in enclosures C_1, C_2, S_1, and S_{10}. The mean abundance of *Leptodora* (0.22 ind·L^{-1}) was 5 times higher in S_{100} than in the other four enclosures. Changes in abundance of *L. kindtii* in the lake were similar to that in C_x. *Chaoborus americanus* larvae were found on most occasions in enclosure S_{100} and the lake but only seldom in other enclosures. On average, *Chaoborus* was 10 times more abundant in S_{100}

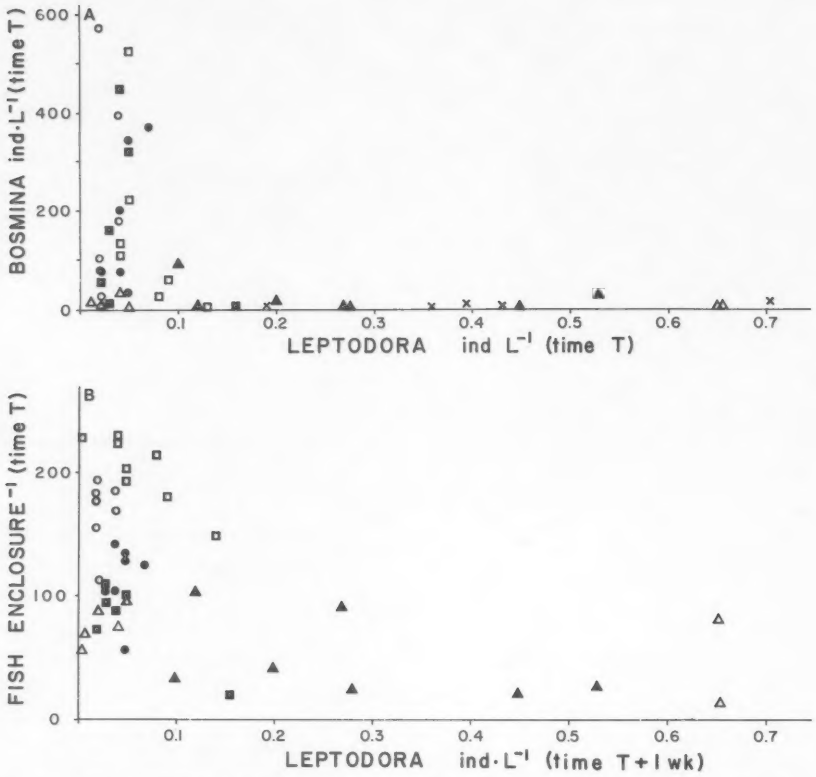

FIG. 6. (A) *Leptodora kindtii* abundance (at time T) vs. *B. longirostris* abundance (at time T) in experimental enclosures and Clay Lake, July 18 – August 27, 1979; (B) *L. kindtii* abundance (at time $T + 1$ wk) vs. fish abundance (at time T) in experimental enclosures. In Fig. 6B, dependent *L. kindtii* abundance is placed on the x-axis for comparison with independent *L. kindtii* in Fig. 6A. The lag time $T + 1$ wk (i.e. following sampling occasion) was assumed to be the period required for *L. kindtii* abundance to exhibit a response to predation by fish present the previous week. ●, C_1; ■, C_2; ▲, C_x; ○, S_1; □, S_{10}; △, S_{100}; ×, lake.

(0.02 ind·L^{-1}) than in other enclosures (0–0.008 ind·L^{-1}). Lake samples contained the highest amounts of *Chaoborus* (mean 0.08 ind·L^{-1}).

A comparison of *B. longirostris* and *L. kindtii* abundances within all enclosures and the lake on each sampling occasion revealed that *Bosmina* were numerous only when fewer than 0.1 *Leptodora*·L^{-1} were present (Fig. 6A). In some enclosures, low *Bosmina* and *Leptodora* abundances cooccurred at the start of the experiment. A similar relationship was found between the number of fish present on a particular sampling occasion (time T) and the abundance of *Leptodora* on the following week (time $T + 1$ wk) (Fig. 6B). High *Leptodora* abundance occurred only when the abundance of fish was low.

The analysis of community similarity revealed two basic temporal patterns among community pairs (Fig. 7). Group 1, which included enclosures C_1, C_2, S_1, and S_{10}, displayed consistently high (>75%) similarities during the study. Group 2 similarities declined over time. In group 2A, communities were relatively similar (50–75%) during the initial 2 wk but then dropped to less than 30% overlap. The lake community (L) was a component of all group 2A pairs. Group 2B pairs exhibited high (>75%) similarity for the first week and then declined rapidly to values between 30 and 50%. All pairs of group 2B included either S_{100} or C_x as a member.

The fecundity of *T. p. mexicanus* declined during the study period in all enclosures and the lake (Fig. 8A). Initially, clutches were similar among all enclosures and the lake. No significant ($P < 0.01$) differences developed among C_1, S_1, and S_{10} in succeeding counts. Fecundities in C_2 and S_{100} were significantly ($P < 0.01$) lower than in C_1, S_1, and S_{10} in the second half of August. The smallest clutches ($P < 0.01$) were carried by females in C_x during August.

Despite declining fecundities, the total number of *T. p. mexicanus* eggs increased in all enclosures during the first 4 wk and peaked between 200 and 300 eggs·L^{-1} in C_2, S_1, S_{10}, and S_{100} (Fig. 8B). In C_1 and C_x, maximum values were between 125 and 150 eggs·L^{-1}. On average, approximately 100 eggs·L^{-1} occurred in enclosures C_2, S_{10}, and S_{100} and from 40 to 70 eggs·L^{-1} in enclosures C_1, C_x, and S_1.

Discussion

Selenium Bioaccumulation

Within the treatment enclosures, net plankton consisting of

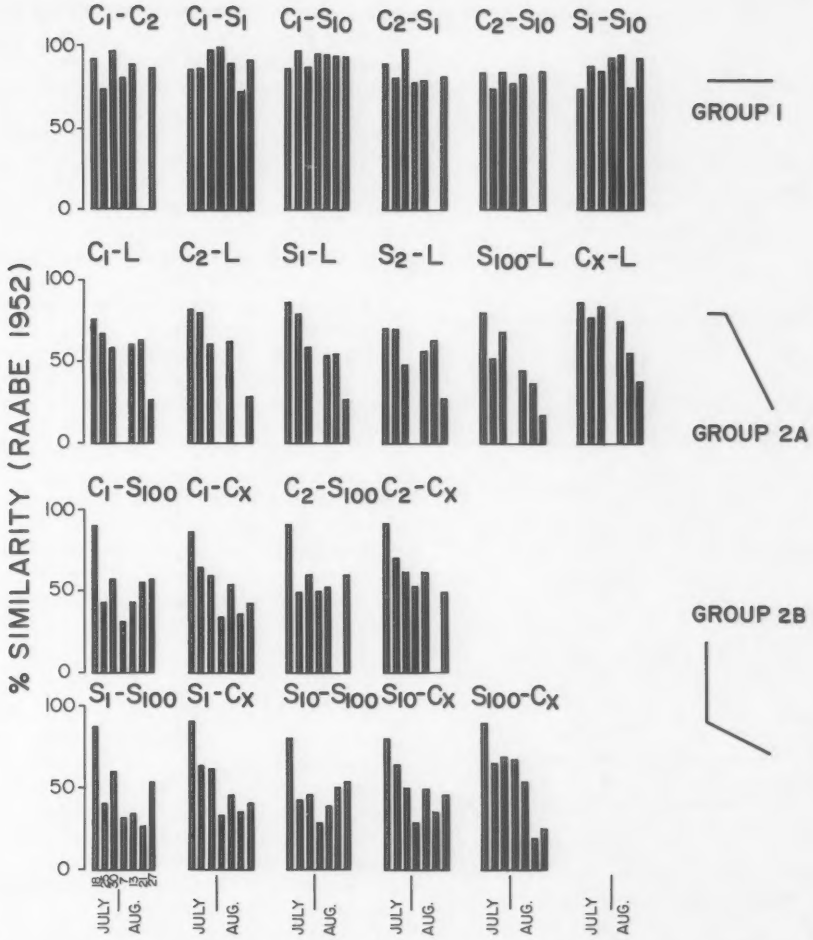

FIG. 7. Seasonal changes in percentage similarity (Raabe 1952) between enclosure pairs or enclosure and lake pairs.

similar amounts of phytoplankton and zooplankton accumulated selenium rapidly in proportion to ambient selenium concentrations. Zooplankton absorb selenium compounds directly from water at concentrations between 1 μg $Se \cdot L^{-1}$ (Sandholm et al. 1973) and 100 μg $Se \cdot L^{-1}$ (Schultz et al. 1980). Selenium may also be ingested by zooplankton during feeding on phytoplankton, protozoans, and detritus. The algae *Scenedesmus* spp. and *Peridinium* spp., present in all enclosures during the experiment, accumulate selenium directly from water (Sandholm et al. 1973; Lindstrom and Rodhe 1978). In spite of selenium bioaccumulation, zooplankton exhibited no apparent toxic effects within the treatment enclosures.

Acute Effects

The high similarity of crustacean community composition (Table 3) and abundance and biomass (Fig. 2) between control and selenium enclosures 2 d after selenium addition indicated a lack of acute selenium effects. The proportions of copepod instars were not visibly altered in treatment enclosures (Fig. 3). Moreover, mature and juvenile daphnids, the latter more sensitive to elevated selenium concentrations (Schultz et al. 1980), were as abundant in the high-selenium enclosure S_{100} on the first sampling occasion as in other enclosures. Percentage similarity was a useful measure of selenium toxicity in spite of variation in initial number of fish. The index was mainly affected by the dominant species of zooplankton which were smaller in size (*T. p. mexicanus*) and not as vulnerable to fish predation.

The lack of an acute effect of selenium on zooplankton within all treatment enclosures was in agreement with the experimental findings of others using sodium selenite. Bringmann and Kunn (1959) determined a 48-h EC50 of 2.5 mg $Se \cdot L^{-1}$ for *Daphnia* sp., which are considered to be the most sensitive crustaceans (Borgmann et al. 1980; McIntosh and Kevern 1974). A similar 48-h LC50 value, 3.87 mg $Se \cdot L^{-1}$, was reported by Reading and Buikema (1983) for *Daphnia pulex*. The much lower static 48-h LC50 values of 0.61, 1.37, and 0.10 mg $Se \cdot L^{-1}$ for fed juvenile, fed adult, and unfed adult *D. pulex* reported by Schultz et al. (1980) may have been affected by crowding stress (25 animals $\cdot 10\,mL^{-1}$) in the test containers. Dunbar et al. (1983) determined the 48-h EC50 for *Daphnia magna* to be 1.1 ±

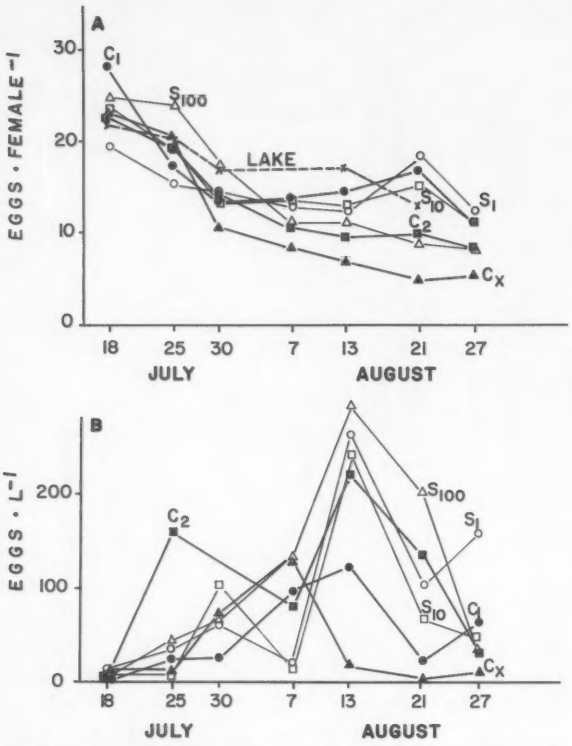

FIG. 8. Changes in *T. p. mexicanus* (A) fecundity (eggs·female^{-1}) and (B) egg totals (eggs·L^{-1}) in control (C_1, ●; C_2, ■), treatment (S_1, ○; S_{10}, □; S_{100}, △), and sediment feedback (C_x, ▲) enclosures and Clay Lake (×), July 18 – August 27, 1979.

0.2 mg Se·L^{-1}. A 48-h LC50 of 0.71 mg Se·L^{-1} was observed for *D. magna* in a continuous-flow system by Halter et al. (1980).

Chronic Effects

Chronic exposure to elevated selenium levels did not appear to adversely affect crustacean community development. Seasonal changes in total abundance were similar in treatment and control enclosures. Abundances rose consistently in all enclosures despite the significant differences in selenium content of zooplankton observed by Turner and Rudd (1983).

The two dominant species, *T. p. mexicanus* and *B. longirostris*, were apparently not affected by chronic exposure to elevated selenium levels. Abundances of *T. p. mexicanus* increased during most of the study with reproduction occurring continuously in all enclosures (Fig. 8A). *Tropocyclops* fecundity was not affected by selenium, as evidenced by clutch sizes which were equivalent in enclosures C_2 and S_{100} and always similar among C_1, S_1, and S_{10}. Declines in *Tropocyclops* fecundity were comparable with those occurring naturally in lakes (Salki 1981) in response to changes in food and population density (Green 1956; Wright 1965; Schindler 1971; Lampert and Schober 1980). In all enclosures the total number of *Tropocyclops* eggs increased through the period of highest selenium concentrations. Similarly, *B. longirostris* displayed no differences ($P < 0.01$) in fecundity among enclosures C_1, C_2, S_1, and S_{10} during the first 4 wk of continuous reproduction and growth. In enclosures C_x and S_{100}, the small populations of *Bosmina* presented insufficient numbers of gravid females to determine fecundities. Other species, however, such as *C. lacustris* demonstrated no reproductive impairment in response to the elevated selenium concentrations in enclosure S_{100}. Throughout the entire study, females carried between 3.2 and 4.9 eggs, similar to the number of eggs produced in enclosures S_1 and S_{10}. In addition, in S_{100}, *D. g. mendotae* and *D. leuchtenbergianum* continuously exhibited constant fecundities which were similar to values in other enclosures. Halter et al. (1980) found that the reproduction of *D. magna* was unaffected by concentrations below 430 μg Se·L^{-1}. No adverse effects on *D. pulex* survival, growth, and reproduction from selenite-Se concentrations below 400 μg·L^{-1} were observed during a 28-d period by Reading and Buikema (1983). However, Reeve et al. (1977) found that *Pseudocalanus* sp. egg numbers were substantially reduced in experimental enclosures contaminated with 5 and 10 μg Cu·L^{-1}.

The elevated selenium concentrations in enclosure S_{100} did not appear to be responsible for the reduced development of *B. longirostris*. A similar seasonal pattern was observed in the sediment feedback enclosure, C_x, as well as in the lake. In addition, in S_{100} the abundances of other cladoceran species, *D. retrocurva*, *D. g. mendotae*, *D. leuchtenbergianum*, and *C. lacustris*, were either higher than or similar to those in other selenium and control enclosures and surpassed those in the lake.

Biotic Interactions

This experiment, designed primarily to determine the toxic effect of selenium on aquatic ecosystems, provided valuable information on the role of biotic interactions in structuring freshwater communities. The initial and subsequent abundances of planktivorous fish significantly affected crustacean community development within the enclosures. Fish directly influenced quantities of larger cladocerans including *L. kindtii*. Subsequently, predatory *Leptodora* controlled the development of *B. longirostris* within the enclosures.

Failure to completely remove all accidently trapped fish prior to the addition of pearl dace and yellow perch led to differences among enclosures which provided an additional, unplanned opportunity to examine the effects of fish predation. On the first sampling date, July 18, large cladocerans (*L. kindtii*, *D. g. mendotae*) were from 5 to 20 times more abundant in low fish predation enclosures C_2, C_x, and S_{100}, which contained 13–23 fish, than in high predation enclosures C_1, S_1, and S_{10} with 57–147 fish. Larger cladocerans such as *Leptodora* and *Daphnia* are among the most preferred food items of planktivorous fish (Brooks and Dodson 1965; O'Brien 1979).

Following addition of pearl dace and yellow perch, both primarily planktivorous (Scott and Crossman 1973), zooplankton continued to exhibit the effects of fish predation. Large species, particularly cladocerans, were much more abundant (5–100 times) in enclosures C_x and S_{100} with lower mean numbers of fish (37 and 68, respectively) than in C_1, C_2, S_1, and S_{10} with higher numbers of fish (116, 82, 168, and 198, respectively). The highest numbers of large filter feeders occurred in enclosure C_x with the lowest abundance of fish. The temporary exchange of water between enclosure C_x and the lake which allowed some of the pearl dace to escape had no apparent effect on crustacean development, since increases in total zooplankton abundance in enclosure C_x were similar to those in other enclosures.

The numbers of *Leptodora* that escaped fish predation subsequently affected the seasonal development of *B. longirostris* within the enclosures. *Leptodora* is recognized as an important predator of smaller crustacean plankton, particularly *Bosmina* (Cummins et al. 1969; Karabin 1974; Gliwicz et al. 1978; Kerfoot and DeMott 1980). Similar high amounts of *Bosmina* among enclosures C_1, C_2, S_1, and S_{10} were clearly related to the low abundance of *Leptodora* common to these enclosures (Fig. 3). In contrast, the very low abundances of *Bosmina* in enclosures C_x and S_{100}, as well as in the lake, could be explained, independently of selenium, by the high levels of *Leptodora* predation in these habitats. Also, in enclosure S_{100} and the lake, higher levels of *C. americanus* larvae, recognized as a predator of *Bosmina* (Fedorenko 1975; Salki 1981), contributed to the reduction of this small cladoceran. *Bosmina* was the only cladoceran, either large or small, to exhibit a distinct reduction in enclosure S_{100}. *Ceriodaphnia lacustris*, by comparison, displayed uniform distribution among the treatment enclosures. Because of its larger size, approximately 1.5–2 times that of *Bosmina*, and projecting fornices, *Ceriodaphnia* was apparently less affected by *Leptodora* predation.

With the variable amounts of fish present, only control and treatment enclosures with similar amounts of fish were compared to assess selenium toxicity on zooplankton. Thus, controls C_1 and C_2, with higher amounts of fish, were used to evaluate the effects of selenium in treatments S_1 and S_{10}, also with similar quantities of fish. Enclosure C_x, and the lake to a certain extent, provided a perspective on the effects of selenium in S_{100}, since all three habitats contained lower numbers of fish.

In enclosure S_{100}, an exceptional increase of *Tropocyclops* occurred during the second half of the study with nauplii forming a significant (54–73%) fraction of the population. This increase was a consequence of lower *Leptodora* abundance during the second half of the experiment. *Leptodora* predation was probably sufficient to control *Bosmina* but insufficient to restrict the smaller, less detectable *Tropocyclops* nauplii.

Some indication of the interaction between zooplankton and phytoplankton was visible in two enclosures, S_{100} and C_2. In enclosure S_{100}, elevated primary production and chlorophyll *a* levels were related to large accumulations of *Anabaena planctonica* and *Aphanizomenon flos-aquae* biomass. This dominance by blue-greens was probably influenced by the extremely abundant immature instars of *T. p. mexicanus*. By selectively grazing small green algae in preference to sheathed *Anabaena* species (McNaught et al. 1980), *T. p. mexicanus* can initiate a succession of cyanophytes (Porter 1973; Porter and Orcutt 1980). The transition to blue-greens did not appear to be a response to nutrient conditions because N/P ratios were comparably high in all enclosures (Table 1). In enclosure C_2, significantly higher Secchi readings than in C_1 ($P < 0.01$) may have resulted from greater abundances of grazers (i.e. *T. p. mexicanus*, *D. oregonensis*, and *C. lacustris*, Fig. 4 and 5), which may be responsible for the clarification of several lakes and ponds (Schindler and Comita 1972; Shapiro 1980).

The differences in zooplankton community structure observed in the high-selenium enclosure (S_{100}) were thus explainable on the basis of trophic interactions and appeared to have no obvious relationship with selenium toxicity. In enclosures C_1, C_2, S_1, and S_2, similar crustacean development demonstrated that selenium concentrations of 1 or 10 $\mu g \cdot L^{-1}$ were not toxic to zooplankton. In enclosure S_{100}, only one cladoceran, *Bosmina*, was less abundant than in other treatment enclosures and its reduced levels, as in enclosure C_x and the lake, could be adequately explained by *Leptodora* and *Chaoborus* predation. Other cladoceran species such as *Ceriodaphnia*, which were less vulnerable to both *Leptodora* and fish predation, were uniformly distributed among treatment enclosures. In addition, in enclosure S_{100}, the fecundities of *Ceriodaphnia* and *Diaphanosoma* were equivalent to levels in other enclosures. These findings did not support the conclusion drawn by Lawrence and Holoka (1983) that elevated selenium concentrations (100 μg $Se \cdot L^{-1}$) were responsible for significant decreases in cladoceran abundance in large enclosures in Clay Lake. Lawrence and Holoka appeared to overlook *Leptodora* predation on *Bosmina* in the large enclosures.

Several significant facts regarding the use of large enclosures for ecosystem experiments came to light in this study. They seem particularly important in view of the growing application of this methodology to ecotoxicological research.

(1) The enclosures, even as large as they were, did not accurately simulate the lake environment. They isolated portions of the lake in which unique communities developed in response to the seminatural conditions established by containment. Crustacean abundances in all control and treatment enclosures were substantially higher than in Clay Lake proper (Table 1). The causes of these increases are not clear but probably involve alteration of light and mixing regimes, surface to volume ratios, and predation strategies.

(2) The direction of community development within the enclosures was largely dependent upon initial filling conditions, in agreement with the findings of Gamble and Davies (1982). Differences in the abundances of fish and invertebrate predators among enclosures led to significant differences in zooplankton community structure. Pilot surveys to establish initial starting conditions, particularly predator–prey ratios, are valuable additions to enclosure experiments.

(3) Although the abiotic and biotic conditions prevailing during the experiment were primarily responsible for community development within enclosure C_x, plankton abundances may have been partially influenced by the history of the enclosure sediments. Containment of the sediment in C_x within a control enclosure during 1978 may have contributed to increased calanoid and cladoceran abundances during 1979. Presumably, zooplankton abundances within the 1978 control were enhanced to the same degree as in the 1979 enclosures (the "enclosure effect"). The resulting greater deposition of calanoid resting eggs and cladoceran ephippia in C_x than in adjoining lake areas, where C_1, C_2, S_1, S_{10}, and S_{100} were eventually installed, could have enhanced abundance in C_x in 1979.

With the growing awareness that species interactions play a more crucial role in natural community organization than assumed originally, in-depth studies at the species level can become critical elements of ecological research design. Attempts to simplify sample analysis by grouping organisms into wider taxonomic units or size classes may lead to an unfortunate diminution of information or perhaps a misinterpretation of results.

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Biology of the Bathylagid Fish, *Leuroglossus schmidti*, in the Strait of Georgia, British Columbia, Canada

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The northern smoothtongue (*Leuroglossus schmidti*), a deep-sea smelt, coexists with Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) in the Strait of Georgia, British Columbia. Their eggs and larvae rank third in abundance, and these three pelagic stocks show marked spatial and temporal overlap in deeper waters, especially during reproduction. Development to hatching occurs in the spring at depths >150 m. Smelt larvae metamorphose at 22 mm standard length (SL), some 90 d from hatching, and juveniles join the adults at depths >200 m by autumn. Larger juveniles mature as 2-yr-olds >50 mm SL. Males seldom live beyond 3 yr or exceed 60 mm SL but females may live ≥5 yr and attain 100 mm SL. Adult sex ratio is 2:3 in favor of females. Larger females are multibatch spawners, 2 batches/yr, with a mean fecundity of 100 eggs·g^{-1}·batch^{-1}. Larval diet includes eggs and early stages of crustaceans dominated by Copepoda. Juveniles and adults fed mainly of polychaetes, amphipods, euphausiids, and calanoid copepods found at depths >100 m. Except for the postlarval and early juvenile stages lasting some 3 mo, the life cycle is pursued at depths >150 m. Their bathypelagic existence in the Strait emphasizes predator avoidance coupled with low fecundity, slow growth, and short life span.

Dans le détroit de Géorgie, en Colombie-Britannique, le leuroglosse luisant (*Leuroglossus schmidti*) coexiste avec la merlu du Pacifique (*Merluccius productus*) et la morue du Pacifique occidental (*Theragra chalcogramma*). Les œufs et les larves occupent le troisième rang en terme d'abondance. Dans les eaux profondes, ces trois stocks pélagiques présentent un chevauchement spatial et temporel marqué surtout pendant la reproduction. L'éclosion des œufs a lieu au printemps à des profondeurs supérieures à 150 m. Environ 90 d après l'éclosion, les larves de leuroglosse se métamorphosent à une longueur standard (LS) de 22 mm; à l'automne, les juvéniles se joignent aux adultes fréquentant des profondeurs supérieures à 200 m. Les plus gros juvéniles atteignent la maturité à 2 ans quand ils mesurent plus de 50 mm LS. Les mâles vivent rarement plus de 3 ans et de dépassent pas 60 mm LS, mais les femelles peuvent atteindre 5 ans ou plus et mesurer 100 mm LS. Chez les adultes, le rapport des sexes s'élève à 2 mâles contre 3 femelles. Les plus grosses femelles frayent deux fois par an; la fécundité moyenne se chiffre à 100 œufs·g^{-1}·ponte^{-1}. Les larves consomment des œufs et des jeunes larves de crustacés, surtout des copépodes, tandis que les juvéniles et les adultes se nourrissent principalement de polychètes, d'amphipodes, d'euphausiacés et de copépodes calanoïdes fréquentant les profondeurs supérieures à 100 m. Sauf pour les post-larves et les premiers stades juvéniles qui durent environ 3 mo, le cycle vital se déroule à des profondeurs supérieures à 150 m. La vie bathypélagique de leuroglosse dans le détroit fait ressortir l'évitement du prédateur accompagné d'une faible fécondité, d'une lente croissance et d'une courte durée de vie.

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The northern smoothtongue (*Leuroglossus schmidti*) is a deep-sea smelt (Bathylagidae), the taxonomic status of which was most recently reviewed by Dunn (1983). Over the outer Continental Shelf, *L. schmidti* ranges from southern British Columbia northward around the Pacific Rim, in the Bering and Okhotsk seas, and as far south in the western Pacific as southern Hokkaido Island (Borodulina 1968). To the south of British Columbia, *L. schmidti* is replaced by *L. stilbius* to the Gulf of California (Peden 1981). Further southward, *L. stilbius* is replaced by the third member of their endemic Pacific genus, *L. urotranus*, which ranges from the Eastern Tropical Pacific to the Peru Trench (Bussing 1965).

Leuroglossus schmidti is not only widely distributed around the Pacific Rim but can be abundant as is attested by localized studies. The larvae were the third most abundant fish larvae in coastal waters of Southeast Alaska (Mattson and Wing 1978), accounting for 4.5% of total catches of larval fish from April to November. Large catches of juveniles and adults were reported in the Bering Sea from deepwater trawling (Borodulina 1968). In offshore waters, it inhabits the bathypelagic and mesopelagic zones to 700 m.

The stock of *L. schmidti* reported on here coexists with stocks of Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) in the Strait of Georgia, a semi-enclosed marine basin exceeding 400 m in depth that separates Vancouver Island from the mainland of British Columbia (Fig. 1).

The biology of the Bathylagidae, including the genus *Leuroglossus*, is relatively unknown. In British Columbia waters, our past knowledge of *L. schmidti* is limited to scattered observations on depth distribution offshore (Taylor 1968). Inshore, the gut contents of adults and the presence of larvae and juveniles in

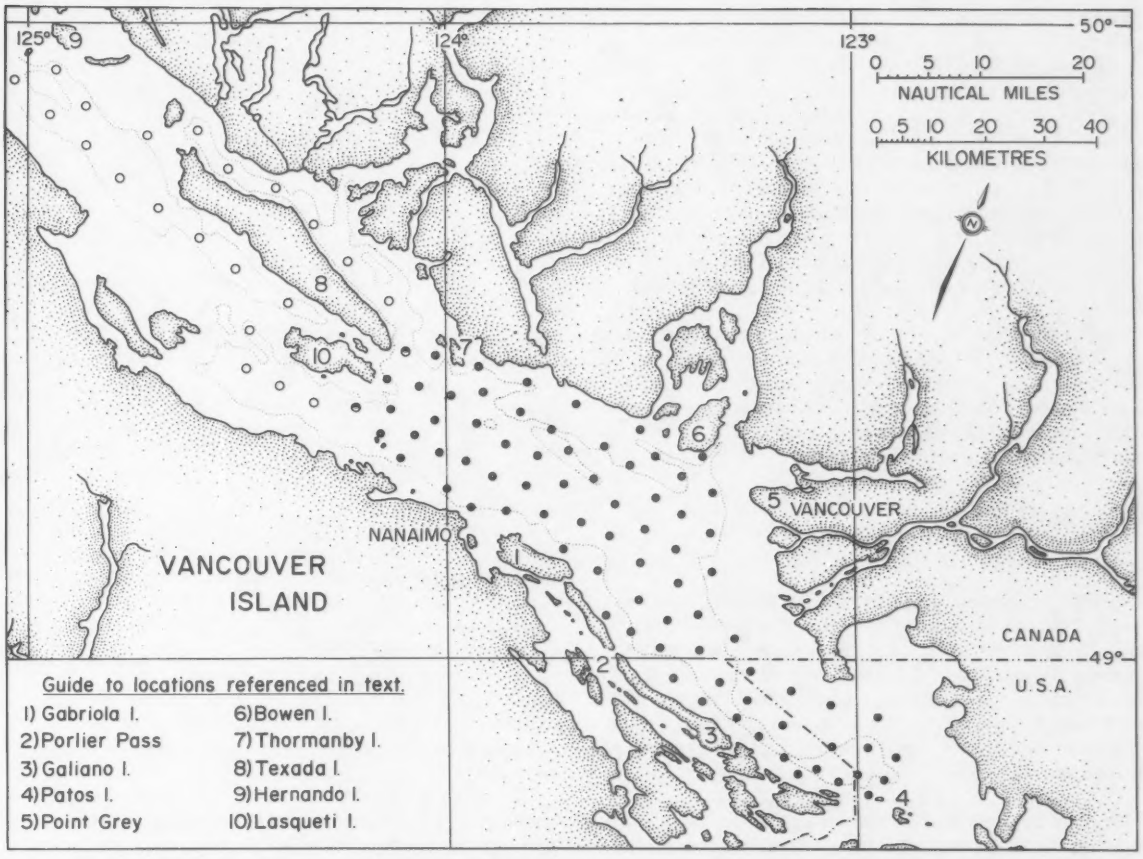

FIG. 1. Strait of Georgia, British Columbia, showing the 1981 sampling grid in the central and southern regions and the transect route through the northern region of the Strait. ◓ = stations common to grid and transect route.

the guts of herring (*Clupea pallasi*), eulachon (*Thaleichthys pacificus*), sandlance (*Ammodytes hexapterus*), and chinook salmon (*Oncorhynchus tshawytscha*) were reported by Barraclough (1967). The present biological account stems from ichthyoplankton surveys dedicated to assessing the stocks of walleye pollock and Pacific hake in the Strait of Georgia from plankton surveys. Eggs and larvae of *L. schmidti* ranked third in abundance behind those of hake and pollock, and both gadids are predators of the smelt. Here, we provide the first information on reproduction, population size and age structure, predator–prey relations, and general life history of a bathylagid stock.

Methods and Materials

Survey Design and Sampling Methodology

A sampling grid of 90 and 80 stations, respectively, for 1980 and 1981, covering the central and southern regions of the Strait of Georgia, was occupied routinely from February to June of both years and supplemented by transect cruises in northern Strait of Georgia (Fig. 1). Reduction of station number involved minor locational changes for <10% of the stations within the common grid. Five complete grid cruises were make at 3-wk intervals in 1980, and nine such cruises in 1981, progressing from northwest to southeast, cruise completion requiring from 7 to 9 d depending on weather. Six cruises on a nine-station minigrid located in the central part of the Strait were made during January–February 1980.

On each station, oblique tows were taken within 5 m of the sea floor, employing 0.25-m^2 Bongo samplers after McGowan and Brown (1966), following the general sampling procedure described by Smith and Richardson (1977) with these exceptions: all sampling components were black; nets were of 351-μm Nitex and of modified SCOR design; codends were of PVC with 351-μm stainless steel mesh windows; a cylindrical weight of 75 kg was suspended 3 m below the nets. Plankton catches were preserved in 5% buffered seawater formaldehyde for analysis ashore (Mason et al. 1982a, 1982b, 1982c, 1982d, 1982e). Catches of *L. schmidti* eggs and larvae were standardized to number per 10 m^2 of sea surface by applying a standard haul factor to the raw catches derived from the following equation:

$$\text{SHF} = \frac{\text{max. tow depth (m)}}{\text{vol. filtered (m}^3\text{)}} \times 10.$$

Vertical profiles of temperature and salinity were obtained at representative stations using a Bisset-Berman STD system, standardized from Nansen casts. Vertical profiles of temperature were obtained routinely at 20 stations covering the grid from XBT casts.

Further information on vertical distribution of the eggs and larvae was collected during March and April 1983 using a BIONESS down-scaled to 0.25 m^2 (MINI-BIONESS) and otherwise modified from the original multinet sampler described by Sameoto et al. (1980). Additional sources of juvenile and adult *L. schmidti* in 1981 included incidental catches in Diamond 5 midwater trawls equipped with 3-cm condend liners (Thompson and McFarlane 1982) and primary catches in a 3 × 8 m midwater trawl with a 1-cm codend mesh. These data sources were supplemented by similar catches made by Barraclough and Herlinveaux (1965) and unpublished data of Barraclough as part of an investigation of sound scattering layers in the Strait of Georgia.

Routine measurements on the sampled fish include total, fork, and standard lengths and blot-dried wet weights to the nearest 0.1 g. Otoliths were extracted from fresh-frozen samples and stored in 50% glycerin–water with thymol and were aged using reflected light. Ovaries were stored in Gilson's solution as modified by Simpson (1951).

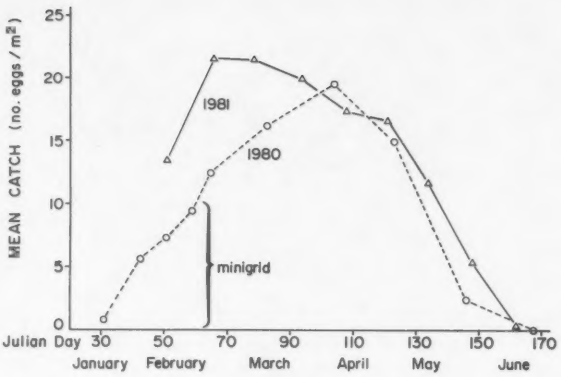

FIG. 2. The 1980 and 1981 spawning cycles of *L. schmidti* in the Strait of Georgia as indicated by the mean density of eggs on individual cruises. The minigrid is composed of a rectangular block of nine stations located in mid-Strait between Nanaimo and Bowen Island.

Results and Discussion

Reproduction

Spawning commenced in late January, peaked during early March (1981) and early April (1980), and ceased by late June (Fig. 2). Most spawning takes place during the 4 mo from February through May. Interannual differences are evident in that, compared with 1980, egg catches peaked earlier in 1981 and annual production of eggs was probably higher, assuming comparable rates during the first half of the spawning season. Temperatures at depths >100 m were slightly higher in 1981 (<0.5°C), which may have advanced reproductive timing.

Sex could be determined in individuals >38 mm SL. Gonads were classified as immature, maturing, ripe, and resting. Ripe testes were swollen and weighed about 10% of total body weight. Ripe ovaries contained eggs 1–1.5 mm in diameter and weighed 15% or more of total body weight. Gonads in the typical "spent" condition, flaccid or bloodshot, were not seen; rather the gonads appeared to be in an "active" state during the spawning season and in a "resting" state in the summer and fall coincident with reduction in size.

Microscopic analysis showed that 37 maturing and more advanced ovaries from females collected in February ($N = 23$) and April ($N = 14$) 1981 contained yolked eggs from 0.08 to 1.5 mm in diameter. Oocytes >1.3 mm in diameter were interpreted as approaching full hydration, as minimum diameter of fertilized, planktonic eggs was 1.36 mm. Total counts of yolked oocytes ranged from 5000 to 8000. Subsamples of 200 eggs from each ovary were measured to provide diameter–frequency distributions. Maturing ovaries contained at least two and as many as four size modes (Fig. 3), with onset of modal definition discernable at oocyte diameters of 0.2–0.3 mm. In ripening ovaries of larger females (>65 mm SL), the two largest size fractions were isolated from each other and from the remainder of the developing oocytes, as in Fig. 3E. Of 34 females >60 mm SL collected in September 1981, the resting ovaries of 10 females examined microscopically showed a single frequency mode <650 μm, as in Fig. 3J.

Leuroglossus schmidti is evidently a multiple spawner, as two or more batches may be produced during the spawning season. The development of the maturing ovary follows the same general pattern reported for Pacific saury (*Cololabis saira*) and several atherinids by MacGregor (1976). The seasonal sequence of batch production begins with a large size mode below 600 μm in diameter beginning to fractionate (Fig. 3A). A fraction of this mode splits off and moves forward to develop into a spawning batch (Fig. 3B, 3C). As this large oocyte fraction proceeds towards hydration and release (Fig. 3D, 3E, 3F), a secondary mode appears and proceeds forward in larger females (Fig. 3C, 3D, 3E). These larger size fractions are presumably spawned and the sequence is arrested before early summer, leaving the single mode usually <500 μm in the resting ovary (Fig. 3J).

Size progression of the first and second modes proceeds at comparable rates of diameter increase prior to hydration once the secondary mode is recognizable (Fig. 4), the mean size of mode two eggs approximating 55–60% of that for mode one.

In 26 ovaries showing double batch production, the number of advanced eggs per batch ranged widely in both size modes. Mean batch size was slightly larger (215) for mode one than for mode two (194) but the difference was not statistically significant by *t*-test. Thus, in larger females (>65 mm SL and 2–4 g weight wet) spawning twice during the season, released egg production was probably about equal at 200–400 eggs /batch in both spawning events. We found no evidence of resorption of advanced eggs, and ovaries containing a few large, hydrated eggs are considered to reflect capture of spawning females.

Multiple spawnings may be restricted to large females. During the spawning season (February–June), females ≥65 mm SL were found more frequently in spawning condition (advanced oocytes) than were smaller females. The smallest maturing female was 54 mm SL and the largest immature female was 61 mm SL. Estimated length at 50% maturity was 59.3 mm SL. Females <60 mm SL containing advanced oocytes were captured predominantly during March and April. At the commencement of spawning in early February, females with advanced oocytes were predominantly ≥65 mm SL. These larger females compose some 55% of the female spawning stock and weigh from 2 to 4 g. Applying the average relative fecundity of 100 $eggs \cdot g^{-1} \cdot batch^{-1}$ and a spawning frequency of 2 batches/yr, the female stock ≥65 mm SL could provide nearly 90% of the annual production of released eggs, the remainder stemming from a single spawning of females <65 mm SL during March and April.

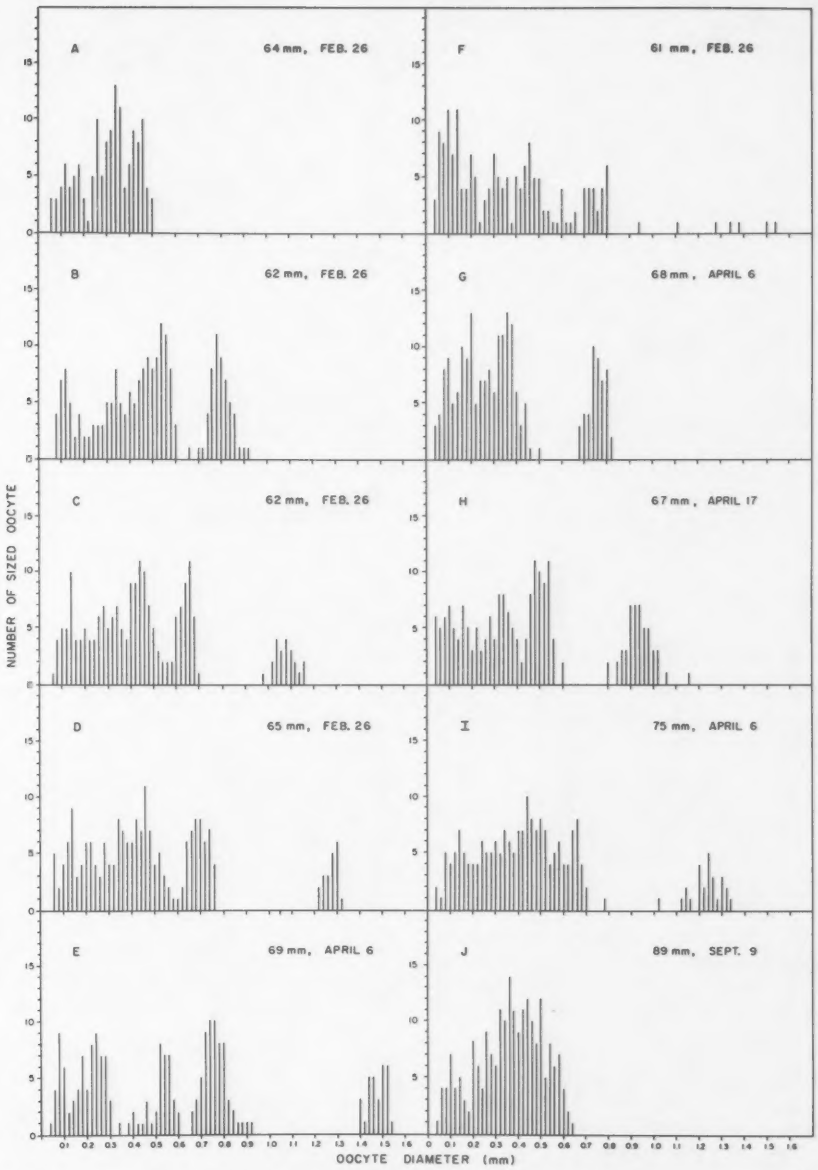

FIG. 3. Representative size frequencies for oocyte diameters in active and resting ovaries of *L. schmidti* from the Strait of Georgia, 1981. Fish lengths are SL.

Mean egg diameter from plankton catches was 1.48 mm (N = 1200), ranging from 1.36 to 1.60 mm. Both range and mean values fall considerably short of those reported by Ahlstrom (1969) for eggs collected offshore between 46°28′–56°28′N and 150°–180′W: 1.65–1.90 mm, with individual collection means ranging from 1.73 to 1.84 mm. Additionally, Ahlstrom (1969) commented on the singular uniformity of egg size within species of *Leuroglossus* and noted the absence of latitudinal or seasonal differences in egg diameter. Investigation of potential differences of spatial or temporal origin that might reflect shifts in the size of female spawners in 1981 revealed no significant differences in egg diameter between areas (north, south, and east) within months (ANOVA F values 0.5–1.7 with 2,∞ df), but differences between months were highly significant (F = 7.5 and 2,∞ df, $P < 0.01$). Mean egg diameter was largest in February, declined to a low in April, and then partly recovered thereafter (Fig. 5). April–June and May–June were the only pair comparisons not different significantly ($P > 0.05$); all other pair F values were associated with P values <0.025. If female size and egg size are positively correlated (untestable with our existing data) and the earlier spawners are also the larger females, such a relationship would support our interpretation of

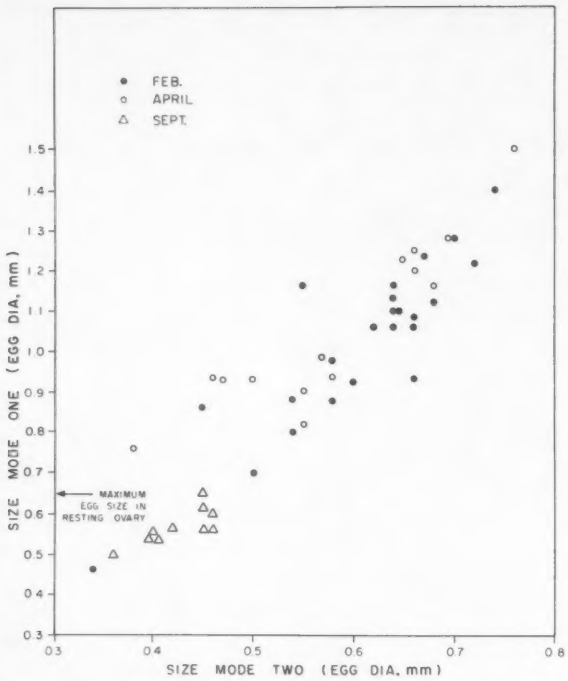

FIG. 4. Progression in mean oocyte diameter within modes one and two, indicating a near-linear relative increase in oocyte size as both modes mature in the ovary of *L. schmidti*.

the seasonal change in mean egg size as stemming from the timing and frequency of batch spawning in females of different size.

Distribution and Abundance

Deeper water areas are preferred for spawning, as is indicated by plotting the annual egg catches on station against station depth (Fig. 6) to which a linear regression model was fitted ($Y = 13.592X - 1879.9$), where $r = 0.87$, Y = number of eggs per $10\,m^2$ per year and X = depth (m). Most spawning took place over station depths exceeding 150 m, and annual catches on station within the sampling grid ranged from near-zero to nearly 5000 eggs$\cdot 10\,m^{-2}\cdot yr^{-1}$.

We limit ourselves to general comments on the vertical distribution of eggs and larvae in the water column, as a detailed account of ichthyoplankton in relation to environment will be published separately. The eggs were most abundant between 200 and 260 m, with few eggs occurring below 300 m or above 150 m. Larvae showed two depth zones of abundance: a major zone between 40 and 90 m and a secondary zone of newly hatched larvae coincident with the egg zone between 200 and 260 m. Most larvae occurred below 40 m during daylight hours of sampling. In summary, the eggs develop and hatch at considerable depth, and hatching is followed by ascension of the larvae to upper waters.

Although *L. schmidti* spawns throughout the various major regions of the Strait, reproductive activity is centered in the central region, bordered to the northwest by Texada and Lasqueti Islands, and to the southeast by a northern line bisecting Galiano Island (Fig. 1). Little spawning takes place in

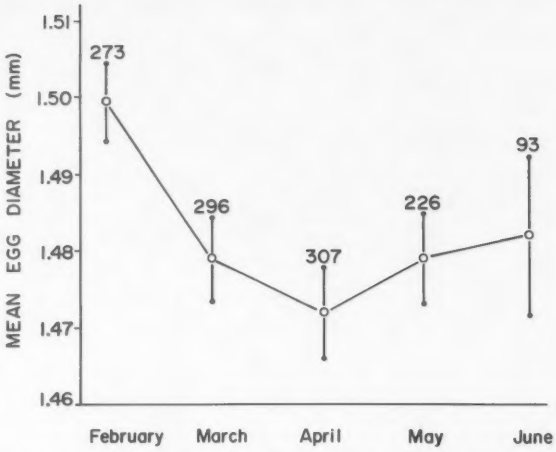

FIG. 5. Changes in the mean diameter of *L. schmidti* eggs in the plankton during the 1981 spawning cycle in the Strait of Georgia. Numbers indicate sample size; vertical bars indicate ±2 SE.

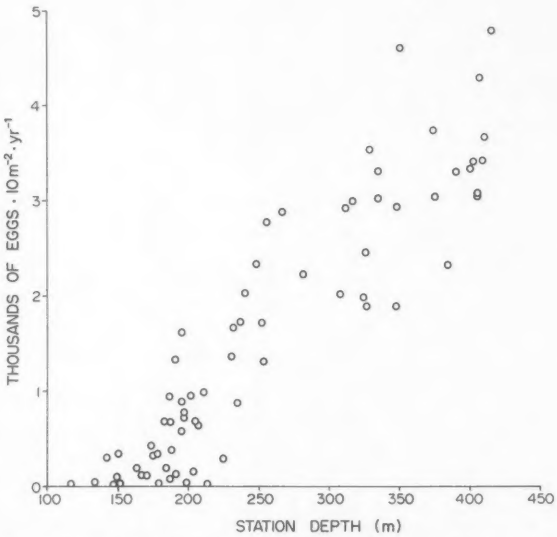

FIG. 6. Relationship between total standardized catch of *L. schmidti* eggs on station and station depth during the 1981 spawning season.

the northern Strait, as is shown by the relative density of eggs during March and April (Fig. 7A, 7C) when most of the spawning occurs (Fig. 2). Thus, the sampling grid adequately captured the main spawning area for the stock in the Strait of Georgia.

In keeping with Fig. 6, the distribution and abundance of eggs, and to a lesser extent larvae, parallels the distribution of waters >200 m throughout the Strait. Highest densities of eggs and larvae were found in waters >250 m (Fig. 7). Larvae were relatively more abundant than were the eggs in nearshore areas on both sides of the Strait in March and April (Fig. 7A, 7B, 7C, 7D), suggesting that onshore transport of larvae takes place. Similarly, larval transport eastward, well beyond the distribution of eggs and towards the edge of the grid at Patos Island (Fig. 1), is evident during March and April. Minor catches of eggs

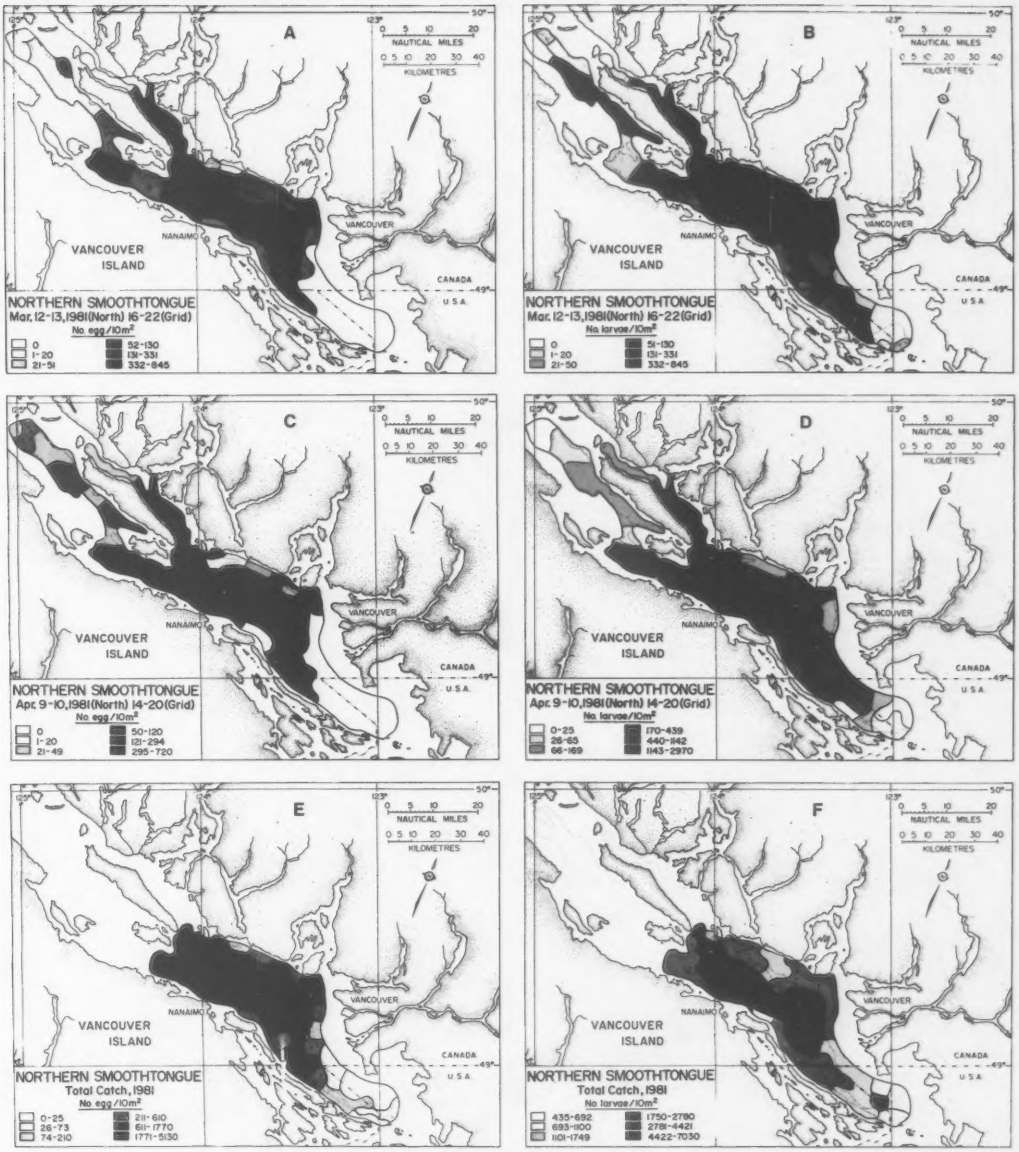

FIG. 7. Distribution and abundance of the eggs and larvae of *L. schmidti* in the Strait of Georgia during the 1981 spawning season. Note that the abundance scales are set by range of abundance encountered in each case.

were made east of Galiano Island on five of the nine grid cruises, primarily associated with the narrow trough of deep water (>200 m) leading into the small eastern basin, but comparable larval catches were 10- to 15-fold higher on an annual basis, as is reflected in Fig. 7E and 7F.

Bongo catches from the ichthyoplankton surveys showed that the adults and juveniles are generally distributed throughout the Strait of Georgia from Hernando Island southeast to the 49th Parallel (Fig. 1) in waters >150 m deep, with highest abundance within the grid, in waters >300 m deep south of Texada Island (Fig. 8A, 8B). Thus, the horizontal distribution of juvenile and adult fish complements the distributions of eggs and early larvae (Fig. 7E, 7F).

Incidental catches of *L. schmidti* taken during midwater trawl surveys for Pacific hake and walleye pollock (McFarlane et al. 1983) and unpublished trawl surveys by Barraclough between 1962 and 1965 substantiate the distributions derived from the ichthyoplankton surveys of 1980 and 1981.

Vertical distribution during daytime was documented off Gabriola Island (Fig. 1) in September 1982 using a 3 × 8 m midwater trawl. Juveniles and adults were distributed between the sea floor (400 m) and 180 m, with juveniles dominating

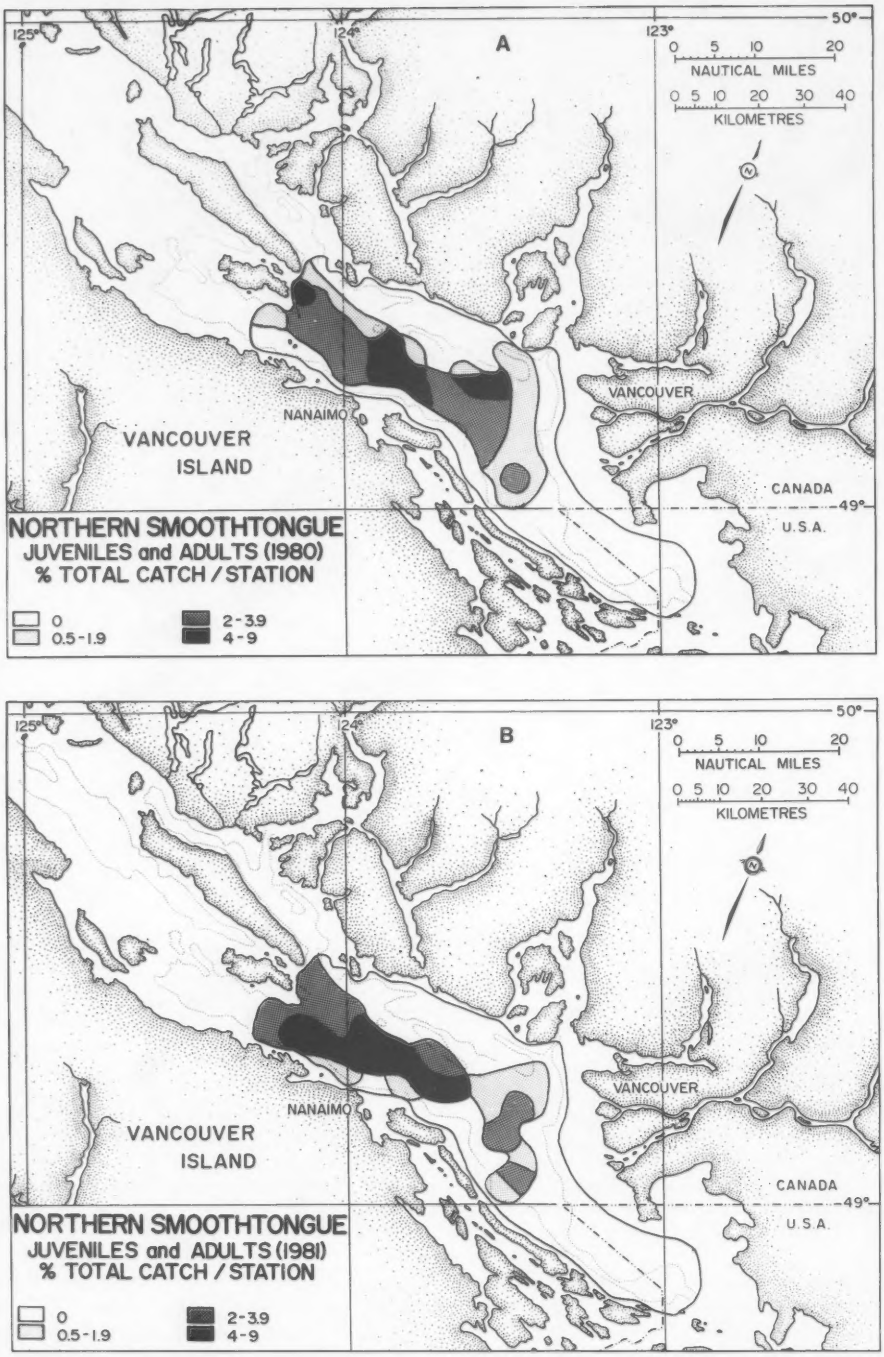

FIG. 8. Distribution and abundance of juvenile and adult *L. schmidti* in the Strait of Georgia during the spawning seasons of 1980 and 1981.

catches above 300 m to the 180-m ceiling. Two 24-h sampling series in April, using MINI-BIONESS in the same area, indicated that juveniles and adults underwent no diel vertical migration and that adults remained at depths below 240 m. Most probably, any translocation over the shallow sills (<60 m except for Seymour Narrows in the north and Haro Strait emptying into Juan de Fuca Strait in the south) is largely confined to the larval stage.

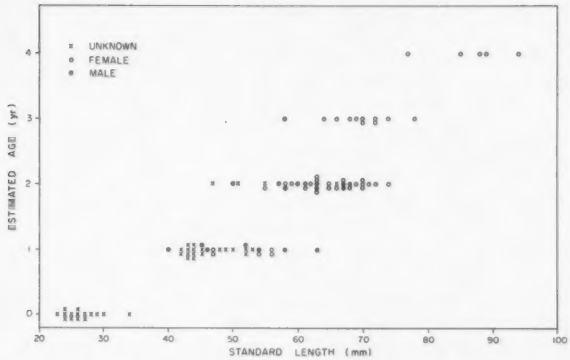

FIG. 9. Distribution of standard length at estimated age (from otoliths) for *L. schmidti* collected in the Strait of Georgia in September. Birthdate is taken as falling within March–April coincident with the annual peak of reproduction, so chronological age is 5–6 mo passed estimated age in years.

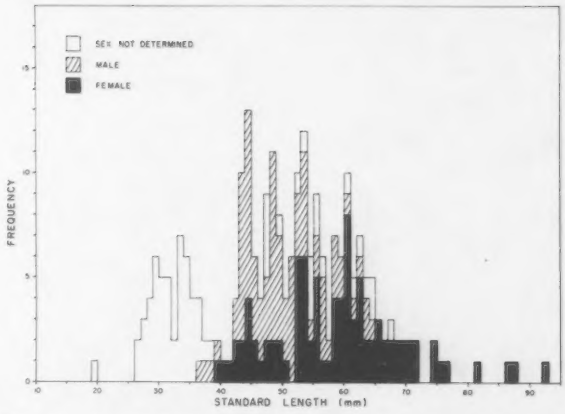

FIG. 10. Length–frequency histogram for midwater trawl collections of *L. schmidti* made in the Strait of Georgia in late February.

Observations made from a submersible (*Pisces IV*) in Jervis Inlet, north of Texada Island (Fig. 1), in May revealed that *L. schmidti* occurred at depths below 175 m to the bottom of the fjord at 620 m. These fish were dispersed and motionless, positioned in a vertical posture with head down, and made no attempt to move away from the submersible (J. Fulton, Pac. Biol. Stn., pers. comm.). This behavior of depth contrasts markedly with the account given by Alldredge et al. (1984) who observed *L. stilbius* at densities of 1–4 fish/m^3 feeding actively on aggregated, diapausing *Calanus pacificus californicus* at 450 m in the Santa Barbara Basin. The *Pisces IV* observation in May predated the seasonal, vertical descent of stage V *Neocalanus plumchrus* approaching diapause in June (Harrison et al. 1983), and no copepod aggregations were observed at depth.

Age and Growth

We aged specimens by counting the number of annuli discernable from surface inspection of the otoliths under a dissecting microscope, using a reflected light source. Otoliths taken from young-of-the-year (age 0) fish, as determined from length–frequency histograms and from developmental characteristics, showed no annulus present in specimens captured prior to the winter but present in February, evidence that the annulus is laid down during the winter. The small size of the otoliths (<2.5 mm in diameter) precluded the use of sectioning techniques although sectioning is unlikely to improve readability, as all otoliths encountered were nearly transparent.

Otoliths read from trawl collections made in September enabled us to discern a maximum of five annuli. Spawning checks were not evident. Increased number of annuli accompanied increased standard length (Fig. 9). Underyearling and yearling fish (age 0 and age 1) and age 3 and 4 fish were well-separated in standard length, but 2- and 3-yr-olds could not be separated by length alone. Only one male was aged beyond its third birthday, confirming the general scarcity of males >60 mm SL in all our collections and those of Barraclough taken between 1962 and 1965. We aged one female at 5+ (85 mm SL), and past collection of females to 101 mm SL suggests that females may live 5 or more yr in this stock.

The aging analysis is partly supported by length–frequency distributions derived from large catches made by midwater

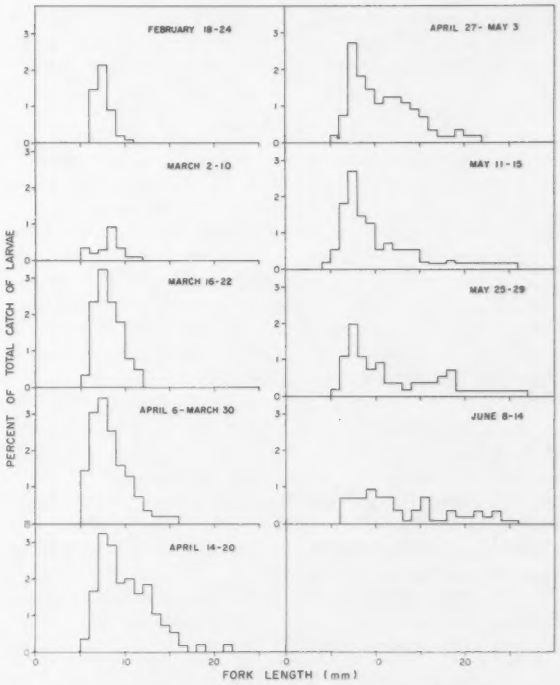

FIG. 11. Length–frequency histograms for the larvae of *L. schmidti* collected from the plankton during the 1981 spawning cycle in the Strait of Georgia.

trawl, but interpretation is hazardous and slow growth compounds the problem. A frequency distribution of midwater trawl catches made in February (Fig. 10) suggests five and possibly six or seven modes, the first bar (20 mm) representing the smallest age 0 approaching their birthday. There is a noticeable lack of males >65 mm SL, as mentioned previously. From our gonadal and aging analyses, we tentatively conclude that both sexes mature as 2-yr-olds, males seldom live beyond 4 yr, and females may attain an age of 5 or 6 yr. Thus, males may breed twice and females three or more times.

Hatching commences in late January at an initial larval length

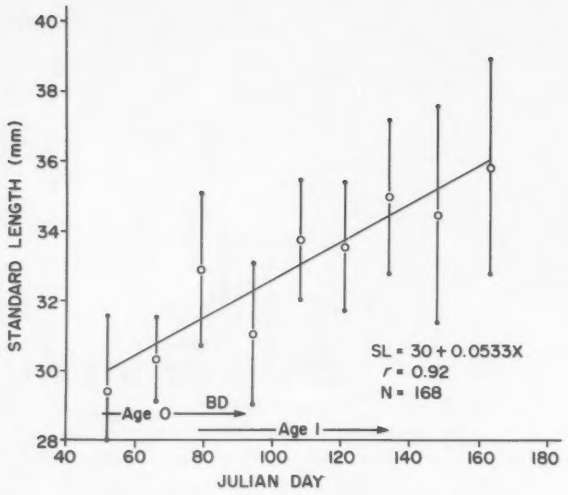

FIG. 12. Linear rate of growth of postlarval and juvenile *L. schmidti* (1980 age class) during the spring and early summer of their second year, 1981. Vertical bars indicate ±2 SE; BD = birthday (Julian day 92).

of 5 mm. Metamorphosis to the juvenile form takes place at 20–24 mm SL, and some 130 d is required to attain a length of 26 mm (Fig. 11), reflecting a maximum daily length increment of 0.16 mm/d[1]. Growth rate slows during the subsequent 8 mo to an average rate of 0.06 mm/d, since smelt start their second year of life at an average length of 32 mm SL (Fig. 12). Growth rate is linear and very slow during the following spring and early summer (Fig. 12), amounting to about 0.17%/d. This growth period coincides with the onset and peaking of the zooplankton bloom. In comparison, young pink salmon (*O. gorbuscha*) of comparable size entering coastal, marine waters during the same season grew some 30–35 times faster, 5.8%/d for the first 30 d (LeBrasseur and Parker 1964). The average growth rate of yearling smelt from their second summer onward (0.06 mm/d) can be reasonably applied to the remainder of the life cycle. Although these growth estimates are rough approximations, the available data are sufficient to illustrate that the species, in these waters at least, grows very slowly.

A geometrica curve describing the SL–weight relationship based on 335 specimens ranging from 20 to 94 mm SL gave the following regression equation:

$$W(\mathrm{g}) = 3.69 \times 10^{-6}\ \mathrm{SL}^{3.167}\ (\mathrm{mm})$$

with a correlation coefficient (r) of 0.99. Unfortunately, lack of data from other locations precludes any regional comparison. The largest *L. schmidti* captured in the Strait of Georgia was a female of 101 mm SL, weighing 7.2 g. A few specimens have been taken incidentally in trawling operations in Dixon Entrance and off the west coasts of the Queen Charlotte Islands in northern British Columbia, their sizes indicating that this species attains a larger size (>200 mm SL) along the outer Continental Shelf and adjoining open ocean. Growth during the early life history at least may be more rapid in offshore waters northward of Vancouver Island than in the Strait, assuming that metamorphosis is primarily a function of age rather than of size. Metamorphosis occurs at 20–24 mm SL in the Strait of Georgia compared with 31–35 mm SL in offshore waters (Dunn 1983).

Population Structure and Stock Size

Our combined catch data for 2 yr of field sampling indicate a sex ratio of 2:3 in favor of females in that portion of the population >38 mm SL, the length at which sex can be determined reliably. Although we were unable to secure sufficient midwater trawl catches to test for seasonal changes in the stability of sex ratio within individual catches, the available data do suggest that marked departures from the 2:3 ratio in large catches (35–235 fish) occurred during the spawning season. Perhaps single-sex aggregations form during the spawning season, ultimately combining to form small spawning schools. If single-sex and spawning aggregations do occur, the striking uniformity in abundance of eggs throughout the deeper waters of the central Strait implies that such aggregations are limited in size and well-dispersed.

The stock present in the deeper waters of the Strait appears to be composed of adult females (~50%) and adult males plus juveniles of both sexes in roughly equal proportions. Recruitment of juveniles to deeper waters occurs in the summer and autumn following metamorphosis, and the entire life cycle appears to take place below 150 m, except for the larval – early juvenile period of some 3–4 mo duration. Although underyearlings compose less than 10% of the catches in the central areas of the Strait in September, their growth rate (Fig. 12) should see larval metamorphosis completed before the late summer, and their poor contribution to mid-Strait catches signifies their continued presence in nearshore areas <150 m deep into the autumn.

Well-documented estimates of the adult stock biomass for 1980 and 1981 based on the released egg production method will be the subject of a separate communication. We estimated the total biomass of the stock in late February 1981 in a preliminary fashion from the distributional data (Fig. 9), the length–frequency histogram constructed from midwater trawl catches (Fig. 11), and the length–weight equation. Using an average body weight of 1.2 g, the stock biomass amounted to 370 Mt in 1981. Using the same mean weight for 1980, stock gave a late winter biomass estimate of 307 Mt.

Predator–Prey Relations

Leuroglossus schmidti is a minor prey of Pacific hake and walleye pollock in the Strait of Georgia composing <2% of stomach contents (by volume) during the spring (McFarlane et al. 1983). Although the smelt may be an even more insignificant dietary constituent of these adult gadid stocks annually, which amount to some 200 250 kt (Mason et al. 1984), potential gadid consumption of smelt could easily exceed the stock size. Dogfish, rockfish, and chinook salmon also eat *L. schmidti* in the Strait. Slow growth, small terminal size, low fecundity, short life span, 150-m distributional ceiling for older juveniles and adults, and abundance of known fish predators in the Strait (est. 4×10^5 Mt), suggest that the bathypelagic habit in Georgia Strait insures perpetuation of the stock.

Identified predators of the eggs and larvae include the carnivorous copepods *Euchaeta elongata* and *Gaidius* sp., the chaetognath *Sagitta elegans*, hydromedusae, and juvenile and adult *L. schmidti* (unpublished data). Most observed predation was on newly hatched larvae.

Larval *Leuroglossus* began feeding on copepod eggs at a length of 7–8 mm. The larval gut frequently contained a string of such eggs apparently passing intact through the gut, a phenomenon also noted for larvae of Pacific herring and walleye

pollock. Larger larvae consumed the nauplii of copepods, cirripeds, decapods, and copepod copepodites. Juvenile and adult *Leuroglossus* during the spring and summer ate, in order of abundance, polychaetes (*Tomopteris* sp.), amphipods (*Cyphocaris*, *Euprimo*, and *Scina*), calanoid copepods (*C. marshalli*, and *N. plumchrus*), euphausiids (*E. pacifica* and *Thysanoessa* sp.), ostracods, early stages of these various crustaceans, and fish eggs. *Leuroglossus* cannibalized its own eggs and ate those of its predator, the walleye pollock.

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Recent Changes in the Inshore Forage Fish of Lake Michigan[1]

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Concerns have been expressed that increasing predatory pressure by salmonids may change the forage fish community of Lake Michigan. A decline in alewife (*Alosa pseudoharengus*), the major forage fish, would be a forewarning of such a change. Our 1973–82 surveys showed that alewife declined 86% in 1980–82; concurrently, rainbow smelt (*Osmerus mordax*) and yellow perch (*Perca flavescens*) increased threefold and fivefold, respectively. Spottail shiner (*Notropis hudsonius*) and trout-perch (*Percopsis omiscomaycus*) showed no long-term changes. Bloater (*Coregonus hoyi*) increased 24-fold since commercial fishing was prohibited in 1976. These trends imply that (1) alewife declined from predatory pressure, (2) alewife suppressed rainbow smelt and yellow perch, presumably by preying on their pelagic larvae, (3) alewife did not substantially affect spottail shiner and trout-perch, presumably because their demersal larvae escaped alewife predation, and (4) overfishing, more than the alewife, suppressed bloater.

La modification possible de la communauté de poissons fourrages du lac Michigan par une prédation accrue de la part des salmonidés fait l'objet de certaines inquiétudes. Une baisse du nombre de gaspareaux (*Alosa pseudoharengus*), principal poisson fourrage, serait un avertissement d'une telle modification. Des relevés menés de 1973 à 1982 ont révélé que le nombre de gaspareaux a baissé de 86 % entre 1980 et 1982; en même temps, l'abondance de l'éperlan arc-en-ciel (*Osmerus mordax*) et de la perchaude (*Perca flavescens*) a respectivement triplé et quintuplé. Le nombre de queues à tache noire (*Notropis hudsonius*) et d'omiscos (*Percopsis omiscomaycus*) n'a pas changé à long terme. Depuis l'interdiction de la pêche commerciale en 1976, le nombre de ciscos de fumage (*Coregonus hoyi*) a été multiplié par 24. Ces tendances montrent que (1) le nombre de gaspareaux a baissé à cause de la prédation accrue; (2) le gaspareau éliminait l'éparlan arc-en-ciel et la perchaude, probablement en s'alimentant de leurs larves pélagiques; (3) le gaspareau n'a pas eu une incidence importante sur le queue à tache noire et l'omisco, probablement parce que leurs larves démersales se sont soustraites à sa prédation et (4) la surpêche plus que le gaspareau a entraîné la disparition du cisco de fumage.

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Major forage fish native to Lake Michigan included several species of coregonids and cottids in deep water, and emerald shiner (*Notropis atherinoides*), lake herring (*Coregonus artedii*), spottail shiner (*N. hudsonius*), trout-perch (*Percopsis omiscomaycus*), and yellow perch (*Perca flavescens*) in shallow water (Moffett 1956; Smith 1970; Wells and McLain 1972; Christie 1974). We define forage fish as those species, mostly small in size, that were historically preyed on or, because of their major biomass levels, may be preyed on by Lake Michigan salmonids. Overfishing and introduced fish species have drastically reduced populations of most native species, especially during the 1940s (Smith 1968). However, except for the coregonids and yellow perch, which were caught commercially, few records exist on these populations (Wells and McLain 1973). In the 1960s, the alewife (*Alosa pseudoharengus*) became the dominant forage fish in deep and shallow water of Lake Michigan. Other abundant species in deep water included bloater (*Coregonus hoyi*), deepwater sculpin (*Myoxocephalus thompsoni*), and slimy sculpin (*Cottus cognatus*), while in shallower water, rainbow smelt (*Osmerus mordax*), yellow perch, spottail shiner, and trout-perch were the major forage species (Wells 1968). In the 1970s, these eight species continued to be the major forage species, with alewife still predominating (Brandt et al. 1980; Crowder and Magnuson 1982; Wells and Jorgenson 1983). With increased stocking of economically valuable salmonids in the 1970s (from 7.4 million fish in 1970 to 16 million in 1980), the current status of forage species has become important to Lake Michigan fishery managers (Stewart et al. 1981). Concerns have been expressed about possible declines in alewife production and the potential for destabilization of the predator–prey system (Christie 1974; Stewart et al. 1981). Additionally, the lack of information on economically unimportant species has been a problem in management of Great Lakes fisheries (Christie 1974).

In this investigation, we document the status of inshore forage species, including the bloater, from 1973 to 1982. As predicted by Smith (1970), and others, alewife declined in Lake Michigan. Coinciding with this decline after 1979, rainbow smelt and yellow perch increased. Bloater also increased substantially, but after 1976, the year commercial fishing for this species was prohibited. Spottail shiner and trout-perch abundances have remained steady.

Methods

Methods are described elsewhere (Jude et al. 1975, 1979) and only a brief description is given here. From April to October, fish were sampled at two inshore (0- to 9-m depths) eastern

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Lake Michigan sites, which were 16 and 24 km south of the St. Joseph River mouth. At both sites, 1-, 6-, and 9-m depths were sampled. At 1 m, fish were collected with a 38 × 1.8 m bag seine of 6.35-mm bar mesh. The seine was hauled parallel to shore a distance of 61 m. Duplicate hauls were taken once a month, day and night. At 6 and 9 m, fish were collected with a 4.9-m bottom trawl of 1.9-cm bar mesh and with 160 × 1.8 m bottom gill nets, each consisting of 12 mesh sizes from 1.3- to 10.2-cm bar mesh. The trawl was towed parallel to shore for 10 min. Duplicate tows, in opposite directions, were taken once per month, day and night. Gill nets were set parallel to shore once per month for approximately 12 h, day and night.

All fish were counted and measured (total length to the nearest millimetre) unless large catches of a species occurred. Fish in large catches were sorted into 3-cm size classes. A subsample was randomly selected and the remaining fish weighed. The total number of fish in the weighed group was estimated from the average weight of fish in the subsample and apportioned to the length intervals of fish in the subsample. Gillnet catches were adjusted to numbers caught per 12 h. Fish were not aged, but young-of-the-year were separated from adults (≥age 1) by examination of modes in length–frequency distributions. Because most alewife yearlings are pelagic in deep water (Brown 1972), they were underrepresented in our catches and therefore we separated them from adults (≥age 2) using length–frequency distributions. Annual fishing effort varied <0.8%, thereby allowing direct comparison of annual catches. Variation in annual catch was calculated by summing the variance between duplicate samples; gillnet catches at similar depths were treated as replicates. Annual sample size was approximately 252.

Results

Adult alewife declined 84% from 1974 to 1977 and then remained steady from 1978 to 1982 (Fig. 1). Young-of-the-year alewife fluctuated between 1973 and 1979 and then declined precipitously in 1980–82 (Fig. 2). The 1980–82 average catch of young-of-the-year and adults was only 14% of the 1973–79 average. The alewife has remained at a low level, as Wells and Hatch (1984) reported that in 1983, the lake-wide biomass of adult (≥age 1) alewife was only 19% of the 1973–82 average.

Yellow perch, on the other hand, showed a dramatic increase concomitant with the alewife decline. Catches of yellow perch, which were small during 1973–79 (see also Wells and Jorgenson 1983), increased in 1980–82 (Fig. 1). In addition, catches of young-of-the-year indicated that very strong year classes were produced in 1980 and 1982 (Fig. 2). Good recruitment in Lake Michigan continued in 1983, as Wells and Hatch (1984) reported that yellow perch reproduction in 1983 was the best since the 1950s. Our 1980–82 average catch of young-of-the-year and adults was almost 5 times greater than the 1973–79 average.

Rainbow smelt also increased in 1980–82 (Fig. 1). The 1980–82 average catch was threefold greater than the 1973–79 average. Wells and Hatch (1984) reported almost a twofold increase in lake-wide biomass of rainbow smelt adults (≥age 1) in 1981–83 compared with 1973–80.

Over the 10 yr, spottail shiner and trout-perch showed no consistent trend (Fig. 1). Both species declined noticeably in 1982 when catches were only 43 and 13% of their respective 10-yr means.

During most of the year, bloater resides deeper than 9 m;

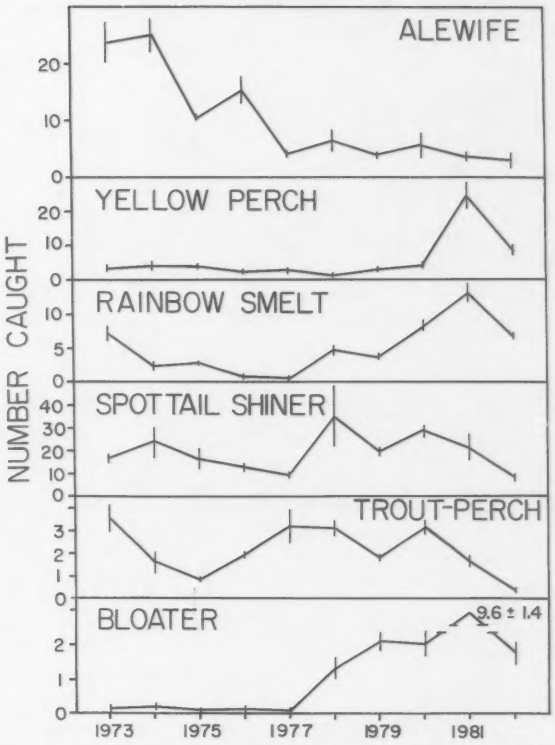

FIG. 1. Total catch (in thousands) of six forage fish in Lake Michigan, 1973–82. Catch is of ≥age 1 fish, except alewife, where catch is of ≥age 2 fish. Vertical lines indicate SD.

however, during summer upwelling, it moves inshore in Lake Michigan (Wells 1968). Our annual inshore catches of adult bloater (≥age 1) correlated significantly (Spearman's rank correlation coefficient = 0.84; $P < 0.05$; $N = 10$) with mean annual lake-wide catches of Wells and Hatch (1984). Consequently, we believe our inshore catches reflect lake-wide abundance. Bloater adults, which were at a low level until 1978, increased and peaked in 1981 (Fig. 1). In addition, after 4 yr of poor recruitment, young-of-the-year bloater increased substantially in 1977 and remained at high levels (Fig. 2). The 1977–82 average catch of young-of-the-year and adults was 24-fold greater than the 1973–76 average. We and others (Great Lakes Fishery Commission 1982) attribute this increase to closure of the commercial fishery in 1976 (Great Lakes Fishery Commission 1979).

Discussion

Because of predation by increasing populations of salmonids, alewife, a species that does not proliferate under high predator pressure (Smith 1968), was predicted to decline in Lake Michigan (Smith 1970; Christie 1974; Stewart et al. 1981). Our results clearly show a decline starting in the early 1980s. Results of lake-wide sampling by Wells and Hatch (1984) corroborate this. They reported a decline after 1981 in adult alewife biomass, which in 1983 was at its lowest level since their sampling began in 1973. Evidently, predator pressure has now reached such intensity that alewife cannot sustain a high

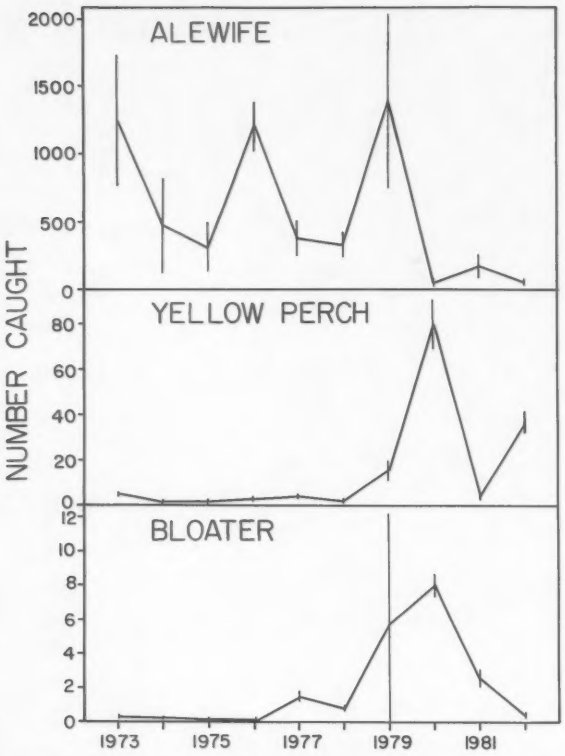

FIG. 2. Total catch (in hundreds) of young-of-the-year alewife, bloater, and yellow perch in Lake Michigan, 1973–82. Vertical lines indicate SD.

population level. Some consequences of a drastic decline to other forage species in the lake are suggested from the changes that occurred when the alewife became established.

That the establishment of the alewife in Lake Michigan caused, or at least contributed the most to, the decline of emerald shiner and yellow perch in the 1950s and 1960s has been persuasively demonstrated (Smith 1970; Wells and McLain 1972; Wells 1977; Crowder 1980). The alewife was also implicated in the declines in some deepwater coregonids, deepwater sculpin, lake herring, lake whitefish (*Coregonus clupeaformis*), and rainbow smelt (Smith 1970; Wells and McLain 1973; Crowder 1980). These latter interrelationships are, however, less understood, especially regarding lake herring and rainbow smelt (Christie 1974). Certainly, as Christie (1974) has suggested, the large biomass of alewife and rainbow smelt would have affected the populations of most native species in the Great Lakes.

Our results show a substantial yellow perch increase and a rainbow smelt increase coinciding with the alewife decline. Wells and Hatch (1984) also reported lake-wide increases in rainbow smelt during 1980–83 and yellow perch in 1983, when reproduction may have been the best since the 1950s. The mechanism for these species' interactions is unknown, but alewife predation on yellow perch larvae has been suggested (Wells 1977; Crowder 1980) and we concur. The apparent lack of interference between alewife and spottail shiner supports this hypothesis. Spottail shiner has shown no long-term changes between 1964 and 1971 (Wells and McLain 1973) or from 1973 to 1982. This stability, especially during the 1960s when alewife reached a peak and then crashed (Brown 1972), existed while a congener, emerald shiner, was decimated. Alewife, emerald shiner, and spottail shiner all spawn inshore during summer (Flittner 1964; Wells 1968; Wells and House 1974; Jude et al. 1979, 1981). For at least part of their early life, emerald shiner larvae are pelagic (Flittner 1964), as are yellow perch larvae (Houde 1969; Wong 1972; Perrone et al. 1983) and rainbow smelt larvae (Tin and Jude 1983), and thus are vulnerable to alewife predation. In addition, alewife predation on fish larvae can be substantial, as the frequency occurrence of larval fish (six species including yellow perch) in alewife stomachs can reach 40–70% (Kohler and Ney 1980). On the other hand, spottail shiner larvae, like adults, are demersal (Jude et al. 1979; 1981) and consequently unavailable to alewife which have difficulty feeding near or on the bottom (Janssen 1978). For similar reasons, trout-perch, which has demersal larvae (Jude et al. 1981), may also have escaped alewife predation.

Although alewife has been implicated in affecting bloater either by competition for planktonic food or by predation on eggs and larvae (Wells and McLain 1972; Crowder 1980), the bloater increase in 1977, 1 yr after closure of the commercial fishery, implies that overfishing has been depressing bloater stocks more than the alewife. Crowder and Magnuson (1982), Great Lakes Fishery Commission (1982), and Wells and Hatch (1984) also indicated that bloater increased in the late 1970s and early 1980s. This coincidence argues for careful regulation of the fishery if reestablishment of a relatively stable forage base of native species is a management goal (Smith 1972; Christie 1974).

Undoubtedly dramatic changes have occurred in the forage species of Lake Michigan, as well as in the zooplankton and algae in the early 1980s (D. Scavia, Great Lakes Environmental Research Laboratory, Ann Arbor, MI 48104, pers. comm.). If the alewife collapses, we suggest that several changes will take place or continue to occur. Bloater, rainbow smelt, and yellow perch should increase if commercial fishing is closely regulated. Deepwater sculpin and emerald shiner could also increase. Deepwater sculpin, another native species with pelagic larvae (Mansfield et al. 1983), did exhibit a substantial increase in 1980 and 1983 (Wells and Hatch 1984). Emerald shiner is at a very low level and has shown no recent changes (Great Lakes Research Division, unpubl. data); several years may be required for its reestablishment. However, the increasing yellow perch population may limit the resurgence of this species, since emerald shiner is preyed upon by yellow perch (Flittner 1964). Spottail shiner and trout-perch are also preyed upon by yellow perch (House and Wells 1973; Nursall 1973; Scott and Crossman 1973; Wells and House 1974) and conceivably, could decline. Both species did decline in 1981 and 1982 when yellow perch increased. Other predator-induced changes in Lake Michigan's forage fish community have been hypothesized and discussed by Stewart et al. (1981). We agree with Stewart et al. (1981) in that careful monitoring is required now so study of current changes can be used to provide insights to resource managers and scientists.

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Energy Flow Between the Pelagic and Benthic Zones: Factors Controlling Particulate Organic Matter Available to an Intertidal Mussel Bed[1]

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Fréchette, M., and E. Bourget. 1985. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. 42: 1158–1165.

Fluctuations and vertical gradients of particulate organic matter (POM, as indicated by chlorophyll *a* and phaeopigments) concentration over an intertidal mussel bed were studied over fortnightly tidal cycles. Chlorophyll *a* variations were not associated with wave amplitude, tidal energy, and sigma-*t*, and phaeopigment concentration was correlated positively with wave amplitude only. Comparison of total pigment concentration in water pumped simultaneously from within 5 cm and from 50 cm above the mussel bed showed significant depletion of POM nearest to the mussel bed throughout the first of the two fortnightly tidal cycles studied. During this period, POM depletion was negatively correlated with current speed, but not with mussel filtration rate, nor with wave energy. During the other period, POM depletion was significant in three of the six semidiurnal tidal cycles studied, and depletion was negatively correlated with wave energy only. Our data indicate that food is often depleted immediately above mussel populations, and that water movement is critical in determining food availability for suspension feeders.

Nous avons étudié les fluctuations semi-mensuelles de la concentration en matière organique particulaire (MOP) et sa répartition verticale au-dessus d'un banc de moules intertidal. Aucune corrélation n'a été observée entre la concentration en chlorophylle *a* et les variables physiques d'intérêt (amplitude des vagues, l'énergie de marée, et sigma-*t*). Par contre, la concentration en phéopigments montre une corrélation positive avec l'amplitude des vagues. La répartition verticale de la concentration totale en pigments, basée sur un échantillonnage à moins de 5 cm et à 50 cm au-dessus du fond, indique une certaine déplétion en MOP immédiatement au-dessus des moules. Cet état de choses se serait maintenu pendant la durée totale d'une première série semi-mensuelle d'observations. Au cours de cette période, l'intensité de la déplétion en MOP près du fond était inversement proportionnelle à la vitesse du courant. Une seconde série semi-mensuelle d'observations révèle le caractère variable de l'intensité de la déplétion près du fond. En effet, celle-ci n'est significative que pour la moitié des observations, et est inversement proportionnelle à l'énergie des vagues. L'ensemble de ces résultats suggère d'une part que la déplétion en MOP au-dessus de suspensivores benthiques pourrait être chose courante, et d'autre part, que les conditions hydrodynamiques joueraient un rôle déterminant dans la disponibilité de la nourriture.

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Energy flow dynamics of benthic suspension feeders are usually examined in relation to an annual cycle (Bayne and Widdows 1978; Widdows et al. 1979; Newell and Bayne 1980; Vahl 1980). Underlying this approach is the assumption that most of the environmental and biotic variability pertaining to the control of energy flow is related to a yearly cycle. Though it may be correct for a variable such as water temperature, this assumption may be questioned for other variables (e.g. phytoplankton). In a number of temperate estuaries, indeed, phytoplankton estival dynamics are characterized by strong short-term variability (see Sinclair et al. 1981; Legendre 1981). Phytoplankton biomass has been seen to peak at fortnightly intervals in the St. Lawrence Estuary (Sinclair 1978; Fortier and Legendre 1979; Demers et al. 1979; Demers and Legendre 1981), in Puget Sound (Sinclair 1978, from the results of Winter et al. 1975), in Saanich Inlet (Legendre 1981, from the results of Takahashi et al. 1977), and in York River Estuary (Webb and D'Elia 1980; Haas et al. 1981).

These fortnightly periods in phytoplankton abundance raise the possibility of periodic pulses of energy flow in estuarine benthic environments. Yet, the problem of coupling energy transfer from the pelagic to the benthic domain is not as straightforward. Benthic filter feeders lie at the bottom of the benthic boundary layer (BBL), where processes occur that can modify the availability of particulate organic matter (POM). On the one hand, resuspension of particles from the bottom is possible, and on the other hand, since consumption occurs at the bottom of the BBL, precisely where water exchange is lowest, local depletion of POM is possible as well. Indeed, calculations by Dame et al. (1980) and Jordan and Valiela (1982) suggest

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that salt marsh suspension feeder populations might be capable of filtering a significant proportion of the tidal prism. Cloern (1982) concluded that grazing by benthic suspension feeders was the primary mechanism controlling south San Francisco Bay phytoplankton biomass during summer and fall. The inclusion of BBL dynamics in these considerations, as advocated by Reiswig (1981), would only have strengthened the hypothesis of POM depletion near its consumers.

Spatial gradients in plankton concentration associated with benthic suspension feeders have indeed been reported. Upstream–downstream gradients were observed in coral reefs (Tranter and George 1969; Glynn 1973) and on mussel beds (Wright et al. 1982). Plankton depletion was observed in experiments simulating field situations with cryptic communities (Buss and Jackson 1981) and mussels (Wildish and Kristmanson 1984). Buss (1979) hypothesized that competition for food through plankton depletion may be a key factor in competitive overgrowth between encrusting bryozoans. In situ studies of vertical concentration of seston above suspension feeders yielded conflicting results. Widdows et al. (1979) found no evidence of depletion or resuspension above a mussel bed, either in total seston or in the proportion of POM in seston. On the other hand, Broom (1982) found that near-bottom water samples contained less chlorophyll *a* and more suspended inorganic particulate matter in an area populated by *Anadara granosa* than in an adjacent, unpopulated area. Comparison between the two studies is difficult, since both were based on a very limited number of observations (respectively 7 and 10), which is obviously too little to cover the wide range of hydrodynamic conditions encountered by a single population. Preliminary observations in the St. Lawrence Estuary (unpublished data) showed that chlorophyll *a* concentration could be significantly lower immediately above the surface of an intertidal mussel bed than higher in the water column. There was also indication of fortnightly variations in the magnitude of the depletion.

Thus, POM available to benthic suspension feeders may differ from that in the pelagic zone, owing to processes associated with the BBL. This study was undertaken (1) to assess the possibility of fortnightly variations in POM available to an estuarine, intertidal mussel bed and (2) to study the role of mussel consumption and BBL dynamics in the control of POM vertical distribution above the mussels.

Materials and Methods

Sampling

Two experiments were carried out above a population of *Mytilus edulis* L. (≈0.5 kg dry weight·m^{-2}) located at Pointe Mitis, St. Lawrence Estuary (Fig. 1). In the first one, we examined the possibility of fortnightly variations of phytoplankton biomass available to the mussels (F series). In the second one, we tested the hypothesis that vertical gradients in POM were present above the mussel bed (G series). Data for both experiments were obtained from groups of six semidiurnal tidal cycles (=tidal "blocks"), each sampled every third day, from one series of spring tides to the next one. Three fortnightly groups were studied in the F series (June, July, and August 1981), and only two in the G series (June and July 1981), owing to sampling difficulties. Since sampling could not be performed simultaneously for both types of experiments, sampling for the G series was initiated 1 d after that of the F series. For each

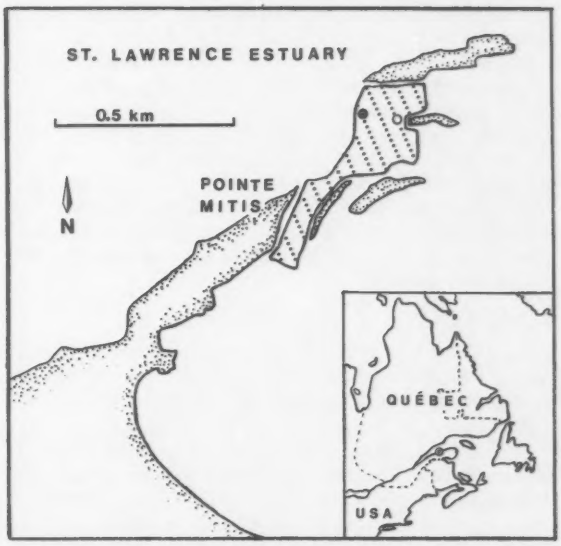

FIG. 1. Study area. Hatched area = mussel bed; ○, midintertidal sampling point; ●, low intertidal sampling point.

group, each of the six blocks consisted on the average of 11 point samples obtained at 20-min intervals from about the end of the flow to midebb. In the F series, water was pumped from within 3–4 cm above the mussel bed at low and midintertidal levels (respectively 1.20 and 2.15 m above zero level, Fig. 1). In the G series, water was pumped from within 3–4 cm (labelled 0.0 m) and from 50 cm (labelled 0.5 m) above the surface of the mussel bed. Water was prefiltered through a 0.75-mm-mesh plankton net which retained larger organisms such as amphipods and benthic macrophytes, but not phytoplankton.

Chlorophyll *a* (250 mL, Whatman GF/C glass fiber filters), methanol-extracted (Holm-Hansen and Riemann 1978), was determined by fluorometry. Chlorophyll *a* was used as an index of phytoplankton biomass. The chlorophyll *a* to phytoplankton biomass ratio is not constant. However, natural populations exhibit a lot less variation in their chlorophyll *a* to biomass ratio than laboratory populations (see Hunter and Laws 1981). Furthermore, the easiness of chlorophyll *a* extraction allows processing a greater number of samples. Since sampling in all blocks was done nearly at the same phase of the semidiurnal tidal cycle, it was assumed that tidally induced variations in the chlorophyll *a* to biomass ratio (Auclair et al. 1982) would not affect between block comparisons. In the G series, water samples were taken simultaneously from the two sampling depths. Since there was no a priori reason to believe that 0.0- and 0.5-m phytoplankton populations were different, the use of chlorophyll *a* in the study of POM vertical depletion did not require the above-mentioned assumptions about the chlorophyll *a* to biomass ratio. Phaeopigments were included in statistical analyses, since they are degradation byproducts of chlorophyll *a*. As such, they were used as a measure of resuspended, previously filtered material. Total pigment concentration (chlorophyll *a* + phaeopigments) was used as an index of POM.

Current speed was monitored using an Aanderaa current-meter equipped with STP probes and fixed near the midintertidal pump. Wave amplitude was estimated visually, using categorical data, and corrected for the height of the water column over

the mussel bed. The resulting variable was termed wave activity (WA).

Filtration rate (V, volume per unit time per mussel weight) was estimated from consumption rate (matter per unit time per mussel weight) (Hildreth and Crisp 1976). Consumption rate was estimated using flow-through techniques. Northby (1976) has cautioned that flow-through measurements with sampling points mounted in series may be biased when input concentration and/or consumption of the rate-indicator substance are not constant, unless storage effects of water in the tank are taken into account. Northby (1976) proposed that consumption at time t (C_t) be estimated as

$$(1)\quad C_t = f[(Qi_t - Qm_t) - \theta(dQm_t/dt)]$$

where f is the flow rate, Qi_t and Qm_t are the concentration of the rate-indicator substance at the input and output of the tank, respectively, θ is the residence time of water in the tank ($\theta \equiv L/f$, L being the volume of the tank), and dQm_t/dt is a correction term allowing for storage effects as water flows through the tank. The correction term may be approximated as $(1/2\Delta t)\,(Qm_{t+\Delta t} - Qm_{t-\Delta t})$ (Northby 1976). Instead of having sampling points mounted in series, it may be preferred to put a control tank in parallel with the experimental tank. Equation 1 can be used for the two tanks simultaneously:

$$(2)\quad C_t - f[(Qi_t - Qm_t) - \theta(dQm_t/dt) = Cb_t - f[(Qi_t - Qb_t) - \theta(dQb_t/dt)].$$

Assuming zero consumption in the control tank ($Cb_t = 0$), that the two flows are equal, and that the experimental organisms occupy a negligible proportion of total tank volume, the equation above reduces to

$$(3)\quad C_t = f[(Qb_t - Qm_t) + \theta(dQb_t/dt - dQm_t/dt)]$$

where Qb_t is the concentration of the rate-indicator substance at the outflow of the control tank and dQb_t/dt is analogous to dQm_t/dt above.

The estimation of the derivatives implies a considerable increase in sampling effort, which one may wish to avoid. Therefore, using data from a related field experiment, we assessed the impact of neglecting the derivatives. Estimations of consumption using Eq. 3 as a whole (C_{AB}) were compared with those obtained using only the first term of Eq. 3 ($C_A = f(Qb_t - Qm_t)$). Experimental conditions were such that residence time was 1.5 min ($L = 1.12$ L) and $\Delta t = 4$ min.

The relationship between the two estimates of consumption was linear (Fig. 2), and its equation was $C_A = 0.975C_{AB} + 0.310$, $n = 70$. The regression coefficient and intercept (model II regression) were not significantly different from 1 and 0, respectively (Clarke 1980). In addition the determination coefficient was $r^2 = 0.94$, which suggests that the derivatives accounted for only a minor proportion of total variance in consumption rate. Therefore, consumption can be estimated as

$$(4)\quad C_t = f(Qb_t - Qm_t)$$

only, with no apparent bias in C_t. We estimated consumption rate using Eq. 4.

Output concentrations from control and experimental filtration chambers were measured by nephelometry, using a Turner Associates model 111 fluorometer. The lower limit of particle size for retention by *M. edulis* is approximately 2 μm (Bayne et al. 1977; Vahl 1972). Nephelometry is sensitive to particles smaller than 2 μm (Eaton et al. 1981), and should particles smaller than 2 μm be abundant, filtration rates would then be underestimated. However, Pointe Mitis is located in a part of the St. Lawrence Estuary where particle size spectra are dominated by plankton peaks, and small particles appear to constitute a negligible proportion of suspended solids (Krank 1979).

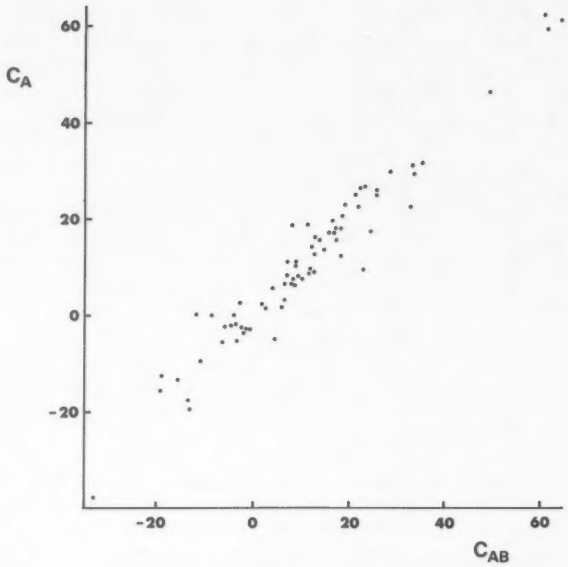

FIG. 2. Scatter diagram between C_A and C_{AB} (fluorescence units·min^{-1}). See text for further explanations.

Six mussels (approximate length 3.5 cm) were used for each of the filtration rate estimations. Between experimental periods, the mussels were kept in situ, near the bottom, in plastic cages. Prior to measuring filtration rates, experimental and control (empty) cages were placed in the appropriate filtration chambers and the animals allowed a 20-min period of acclimation. Disturbance of the animals was thus minimized.

Numerical Analysis

F series

F series chlorophyll *a*, phaeopigments, and physical data were averaged for each tidal block. Tidal energy (TE) was estimated as the variance of predicted tidal heights for each block and the three preceding tides (two lows, one high). This procedure allowed control for diurnal inequality in tidal amplitude. Data were analysed using Pearson's (r) partial correlations.

G series

Since sampling procedures allowed pairwise statistical analysis of data, the hypothesis of vertical depletion of POM within each block was examined comparing total pigment concentration at 0.0 and 0.5 m, using Wilcoxon's signed ranks test (Conover 1980). In addition, the permanence of depletion within each group of blocks was examined using the following procedure, derived from Wilcoxon's signed ranks test. For each of the blocks within a group, the value of the Wilcoxon statistics (T_i^+), the mean ($n_i(n_i + 1)/4$) and the standard error ($((n_i(n_i + 1)\,(2n_i + 1))^{0.5}$) were weighted according to the number of observations plus one ($n_i + 1$). Subtracting the mean from the weighted T_i^+ and dividing by the standard error yielded the Ws_i, normally distributed, with a mean = 0 and a variance = 1. The resulting formula for the Ws_i is

$$Ws_i = \frac{\frac{T_i^+}{n_i + 1} - \frac{n_i}{4}}{\left[\frac{n_i(2n_i + 1)}{24(n_i + 1)}\right]^{0.5}}.$$

The expression

$$\sum_i^k = \frac{Ws_i}{k},$$

where k is the number of blocks within a group, is also normally distributed, with a mean = 0 and a variance = 1. It was used as the test statistic of within group sustained trend in depletion. This extension of Wilcoxon's signed ranks test was preferred to a two-day ANOVA because classical ANOVA procedures preclude pairwise analysis of data and would therefore have resulted in a less powerful test.

The effect of factors presumably controlling the magnitude of depletion was studied using Kendall's τ. This nonparametric correlation coefficient was used because of the apparent nonlinearity of some of the relationships. It is not known how to test partial τ's (Conover 1980). Simple and corresponding partial τ's were nonetheless compared, in order to assess whether caution should be advised when interpreting significant simple τ's.

Current measurements at shallow depths are contaminated by surface waves. The procedure outlined hereafter removed all apparent correlation between these two variables: (1) The relationship between average current observed (U_{obs}) and tidal energy (TE) was determined from measurements made in calm weather, with waves 10 cm or less; (2) from this relationship, the average tidal energy contribution ($\hat{u}$) to U_{obs} was predicted for all blocks, assuming that discrepancies between actual and predicted tidal heights were negligible; (3) next, wave contribution (U_w) to U_{obs} was determined as $U_w = U_{obs} - \hat{u}$; (4) using these estimates, a least squares multiple linear regression was used to derive the relationship between U_{obs}, $\hat{u}$, and U_w. The resulting equation was $U_{obs} = 2.89(TE) + 12.39 \log (WA + 1) + 6.91$. For the purpose of data analysis, wave energy was defined as UVA = 12.39 log (WA + 1); current was defined as $U = U_{obs} - UVA$.

Results

Fortnightly Variations in POM: F Series

Total pigments from lower and midintertidal levels were closely correlated (Fig. 3A, $r = 0.966$, $P < 0.01$, $n = 16$). The relationships between chlorophyll *a* and phaeopigment concentration and the physical environment were studied separately. The physical variables used were wave activity (WA), tidal energy (TE), tidal energy 3 d before the observations (TE3, to test for lag responses in pigment concentration), and sigma-*t* (to test for water mass differences). Wave activity was correlated with phaeopigment concentration at both tidal levels, but only with chlorophyll *a* concentration at midintertidal level (Table 1).

Vertical Distribution of POM: G Series

Total pigments at 0.0 and 0.5 m varied similarly (Fig. 3B). Total pigment concentration appeared to be lower near the bottom in blocks 13, 16, and 17 and blocks 20, 21, and 23 (Table 2). The extension of Wilcoxon's signed ranks test developed above indicated significantly higher total pigment concentration at 0.5 m than at 0.0 m throughout the first group of blocks ($P < 0.01$), but not in the second group ($P > 0.05$).

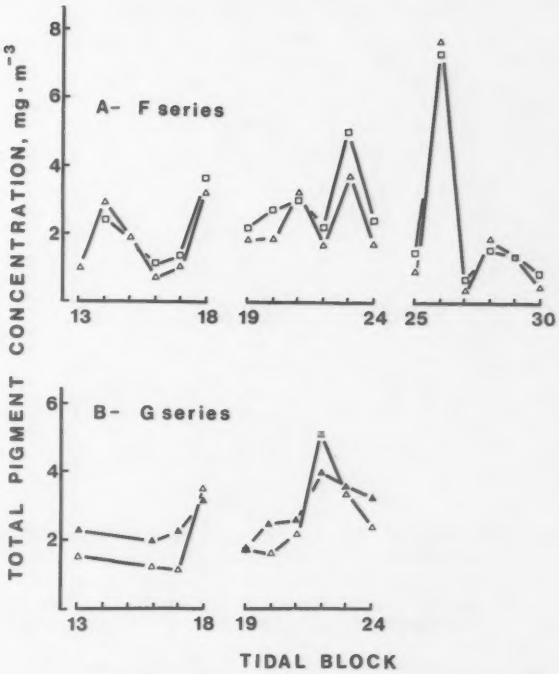

FIG. 3. Mean total pigment concentration (chlorophyll *a* + phaeopigments) (A) F series: △, midintertidal; □, low intertidal; (B) G series: △, sampling from within 5 cm of the bottom; ▲, sampling from 50 cm above the bottom.

TABLE 1. Relationships between pigment concentrations (chla = chlorophyll *a*; php = phaeopigments) and physical variables as given by partial Pearson's correlation coefficients. *$P < 0.05$; **$P < 0.01$.

Shore level	Pigment	Wave amplitude	Tidal energy	TE3	Sigma-*t*
Low intertidal	chla	0.221	−0.086	0.038	0.127
	php	0.681**	0.113	0.054	0.091
Mid intertidal	chla	0.512*	−0.147	0.272	0.095
	php	0.788**	0.200	−0.222	0.221

The control of the magnitude of POM depletion was studied using the 05:00 ratio of total pigments (total pigments at 0.5 m per total pigments at 0.0 m), current speed (U), wave energy (UVA), and filtration rate (V) as defined above (see Materials and Methods). The correlation matrices for both groups of blocks are shown in Table 3. Simple τ's did not differ greatly from their partial counterparts. In the first group (blocks 13, 16, 17, and 18), a significant negative association was found between the 05:00 pigment ratio and current speed only. In the second group (blocks 19–24), the only significant association was a negative correlation between the 05:00 pigment ratio and wave energy.

The mechanisms controlling POM vertical distribution were further examined using chlorophyll *a* and phaeopigment concentrations (Fig. 3). Chlorophyll *a* concentration at 0.0 m was always lower or equal to that at 0.5 m, irrespective of weather

TABLE 2. Outcome of Wilcoxon's signed ranks test (T^+) under the null hypothesis of no difference between 0.0 and 0.5 m total pigment concentration. N = number of pairs of observations; $*P < 0.05$; $**P < 0.01$.

Experimental block	T^+	N
13	36**	8
14	—	—
15	—	—
16	21**	6
17	28**	7
18	12	9
19	38.5	12
20	70*	12
21	65*	12
22	10	10
23	40*	9
24	8	7

TABLE 3. Simple Kendall's correlation coefficients (τ) between 05:00 total pigment ratios (CP), current speed (U), wave energy (UVA), and mussel filtration rate (V). Horizontal headings for tidal blocks 13–18, n = 33. Vertical headings for tidal blocks 19–24, n = 67. Partial correlation coefficients for significant relationships were of slightly higher absolute value. $**P < 0.01$.

	CP	U	UVA	V
CP	—	−0.291**	−0.161	−0.072
U	−0.097	—	−0.032	0.026
UVA	−0.301**	0.002	—	−0.017
V	0.038	0.119	0.042	—

conditions. In contrast, vertical distribution of phaeopigment concentration was obviously sensitive to weather. In blocks 18, 22, and 23, rough weather was associated with increases in phaeopigment concentration (1 mg·m^{-3} and over). Values were noticeably higher at 0.0 m than at 0.5 m. However, none of this was apparent in block 16, despite rough weather (Fig. 4). In the first group of blocks, the 05:00 ratio for chlorophyll a was negatively correlated with current speed, but that for phaeopigments was not (Table 4). The correlation coefficient between the 05:00 phaeopigment ratios and wave energy approached significance (P = 0.054) and increased slightly when mussel filtration rate and current were controlled for. In the second group of blocks, 05:00 ratios for chlorophyll a and phaeopigments were negatively correlated with wave activity.

Discussion

Fortnightly Tidal Cycles

The strong similarity between variations in total pigments at low and midtide levels (Fig. 3A) suggests that whatever process(es) control food availability for mussels (POM), their influence is relevant over a significant area, if not all, of the mussel bed.

The only variable correlated with pigment concentration was wave energy (Table 1). Since chlorophyll a concentration and

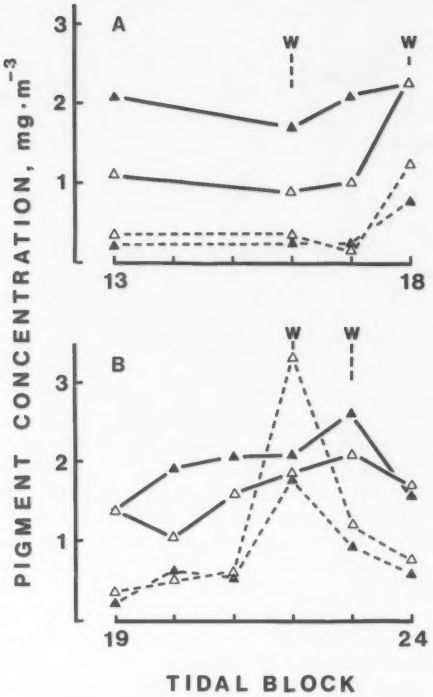

FIG. 4. G series. Mean chlorophyll a (—) and phaeopigments (---) concentration at 0.0 (△) and 0.5 m (▲) above the bottom. (A) Tidal blocks 13–18; (B) tidal blocks 19–24. W = wind events.

TABLE 4. Simple Kendall's correlation coefficients (τ) between 05:00 ratio of chlorophyll a concentration (chla 05:00) and phaeopigment concentration (php 05:00) with current speed (U), wave energy (UVA), and mussel filtration rate (V). Partial correlation coefficients for significant relationships were of slightly higher absolute value. $*P < 0.05$; $**P < 0.01$.

	php 05:00	U	UVA	V
	Tidal blocks 13–18; n = 33			
chla 05:00	—	−0.287*	−0.097	0.069
U	−0.168	—	−0.032	0.028
UVA	−0.216	−0.032	—	−0.014
V	−0.029	0.028	−0.014	—
	Tidal blocks 19–24, n = 67			
chla 05:00	—	−0.086	−0.198*	0.102
U	−0.055	—	0.042	0.119
UVA	−0.248**	0.042	—	0.002
V	−0.065	0.119	0.002	—

tidal energy appear unrelated, it is unlikely that chlorophyll a concentration at the bottom of the benthic boundary layer varied according to fortnightly cycles. There is some indication in Fig. 4 that variations in chlorophyll a concentration in the pelagic zone (0.5 m) can be tracked fairly well in BBL (0.0 m) chlorophyll a concentration. This suggests that the expected neap tide maximum in chlorophyll a may not be a consistent feature (e.g.

Legendre et al. 1982), at least near the shore. This conclusion is valid insofar as the 0.5-m chlorophyll *a* concentration is more dependent on pelagic processes than on BBL processes. In an experiment carried out in 1982 (unpublished), acetone-extracted fluorescence from 0.0 to 0.5 m averaged respectively 54 and 89% of the values obtained 1.0 m above the bottom. Therefore, it appears that POM at 0.5 m above the bottom is influenced mainly by pelagic conditions, though for practical purposes, the BBL above the mussel bed can probably be considered to be of the order of about 1 m thick. Therefore, if any fortnightly variations were present, these were probably of too small amplitude to be detected. Ideally, cycles should be studied using time-series techniques. Such a strategy was not adopted in this study because of the tremendous logistic effort involved. The association between chlorophyll *a* and wave energy is not attributable to resuspension, as its concentration was not higher at 0.0 m than at 0.5 m on windy days (Fig. 4). This suggests that wind increased available chlorophyll *a* mainly by increasing turbulence in the water column and breaking down vertical gradients in phytoplankton (Table 4). The apparent failure of this mechanism to be efficient at low shore level may be attributable to the presence of macrophytes, which may have buffered the effect of waves by changing flow conditions near the bottom.

The strong association between phaeopigment concentration and wave energy (Table 1) probably resulted from the resuspension of sedimented or previously filtered phytoplankton, rejected as pseudofaeces (Kiørboe and Møhlenberg 1981), or possibly also as undigested faeces (Hildreth 1980). Higher levels of phaeopigments nearest to the mussel bed during windy days are consistent with the resuspension of faecal/pseudofaecal matter hypothesis (Fig. 4). Microphytobenthos (and probably also its decomposition byproducts) presumably only accounted for a minor proportion of resuspended POM, since the bottom was not a source of chlorophyll *a* on windy days (Fig. 4). The highest seston concentration encountered during our experiments was $36.7\,mg \cdot L^{-1}$. Since consumption in *M. edulis* increases linearly with seston concentration in those ranges (Widdows et al. 1979; Kiørboe et al. 1980), there is no reason to believe that consumption might have been impaired during resuspension events. This is supported by our own measurements of filtration rates (unpublished). Therefore, it appears that significant amounts of biodeposited POM are resuspended by waves and are likely to be refiltered and assimilated (Kiørboe et al. 1981) by the mussels.

Vertical Distribution of POM

The extent of POM depletion can be appreciated from Fig. 3B. Depletion occurred nearly throughout the first group of tidal blocks but only half of the time in the second group. The intensity of depletion was sensitive to currents and waves. The weaker the currents or wave energy, the stronger the depletion. It is not clear why the influence of current speed on depletion was apparent only in the first group or why wave effects were significant only in the second group, since wind events occurred during the first period (blocks 16 and 18) as well as during the second period (blocks 22 and 23). During sampling block 16, waves were from an easterly direction, and no resuspension occurred, while for blocks 18, 22, and 23, waves were from north and northwest, and resuspension did occur. Wind direction, in conjunction with local topography, might have reduced the effectiveness of waves in breaking vertical gradients and resuspending sedimented particles during block 16 (Fig. 4A, 4B). Despite poor resuspension in block 16, it is noteworthy that the correlation between wave energy and phaeopigment resuspension during the first group of blocks closely approached significance. This may be attributed to strong resuspension in block 18. The reasons why current speed had no apparent influence on the intensity of depletion during blocks 19–24 are obscure.

Unexpectedly, POM depletion was not associated with filtration rate. This may have resulted from time scale differences between the feeding response of mussels and processes controlling phytoplankton replenishment in the BBL. Replenishment is effected through advection and/or diffusion. The relative importance of the two processes remains unknown, but a greater role of diffusion would stress the importance of small spatiotemporal scales in replenishment dynamics (Heathershaw 1974).

Our results show that vertical POM depletion can occur frequently immediately above a suspension feeder population, and also that the vertical gradient can be destroyed by waves and currents or even inverted by the input of mechanical energy of waves. This might explain why previous studies on food depletion in the water column yielded conflicting results (Widdows et al. 1979; Broom 1982). Seston depletion above suspension feeders has been observed in flume experiments (Wildish and Kristmanson 1984) and is implicit in Kautsky's (1982) results. Our data also support the idea that food is often depleted immediately above suspension feeder populations and that hydrodynamic processes are critical in determining food availability (Wildish and Kristmanson 1979). Depletion itself is by no means a proof that mussel growth was limited by food availability. However, present knowledge of mussel response to high food concentration suggests that it might have been the case (Winter and Langton 1976; Paul et al. 1978). This hypothesis will be examined elsewhere (Fréchette and Bourget 1985).

In a study of in situ respiration of a wave-protected mussel bed, Nixon et al. (1971) found that respiration increased with current speed. On the basis of Theede's (1963) work (in Nixon et al. 1971), they argued the possible influence of current on respiration through enhanced metabolic costs of pumping more water at higher current speeds. However, Hildreth (1976) and Hildreth and Crisp (1976) found no evidence that filtration rate is directly dependent on water movement around *M. edulis*. Our results show that in the absence of waves, and all other things being equal, POM available to mussels will increase with increasing current through the decrease of POM vertical gradient steepness (Table 3). Since respiration increases with ingestion, itself enhanced by higher POM concentration (Bayne et al. 1976), it is likely that the correlation between respiration and current observed by Nixon et al. (1971) resulted from increased POM availability.

Input of mechanical energy of waves and currents counteracts POM depletion. This stresses the importance of auxiliary energy input in energy flow (Odum 1967; Margalef 1979). Currents and waves tend to break down spatial segregation between phytoplankton and mussels, thus increasing the availability of food resources for consumers. In addition, as suggested by Griffiths and King (1979) (see also Wulff and Field 1983), resuspension of deposited, incompletely digested food recycles energy directly for consumption, thus increasing energy transfer efficiency between phytoplankton and mussels.

Acknowledgments

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Food-Limited Growth of *Mytilus edulis* L. in Relation to the Benthic Boundary Layer[1]

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Fréchette, M., and E. Bourget. 1985. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer. Can. J. Fish. Aquat. Sci. 42: 1166–1170.

The hypothesis that depletion of organic particles near the sediment limits the growth of benthic suspension feeders was tested. In situ growth of *Mytilus edulis* L. was significantly depressed at the sediment–water interface, as compared with growth 1.0 m above the mussel bed, in studies at two shore levels. Flesh dry weight was sensitive to treatment effects, but not shell growth. We conclude that mussels from the bed were food limited.

Cette étude porte sur l'effet de la déplétion en matière organique particulaire consécutive à son passage au-dessus d'un banc de moules bleues, *Mytilus edulis* L., sur le taux de croissance de la moule. Des individus ont été placés dans des paniers fixés à 1,0 m du substrat et à la surface du banc, aux niveaux moyen et inférieur de l'étage médiolittoral. Le poids sec de chair et l'allongement de la coquille sont utilisés comme indicateurs de croissance. Les traitements expérimentaux n'ont un effet significatif que sur le poids de chair, les moules provenant de la surface du banc ayant un poids de chair inférieur à celles suspendues à 1,0 m du fond. Il appert que la biomasse individuelle est limitée par la nourriture.

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In spite of some experimental results suggesting that competition for food might occur in benthic suspension feeders (Crisp 1960), the opposite view has prevailed (Knight-Jones and Moyse 1961; Levinton 1972). Indeed, it has been argued that plankton abundance is so unpredictable that exploitation competition is unlikely ever to occur, especially in temperate environments (Levinton 1972). However, Levinton (1972) did not dismiss altogether the possibility of competition for food among suspension feeders in constant environments as, for instance, subtidal tropical environments. Indeed, Buss (1979) found evidence that the outcome of competition for space between two encrusting bryozoans may be mediated through competition for food, at least under laboratory conditions. Buss and Jackson (1981) also found strong depletion in plankton available to cryptic organisms settled on artificial substrates. They hypothesized that this could result in competition for food in dense assemblages of suspension feeders.

The importance of food competition for benthic suspension feeders in fluctuating environments is rapidly gaining support. Wildish (1977) and Wildish and Kristmanson (1979, 1984) argued that food limitation of suspension feeders might be more widespread and significant to benthic community dynamics than generally thought. Stiven and Kuenzler (1979) concluded that growth of *Geukensia demissa* was food limited in at least one of the three salt marsh populations studied. Broom (1982) found indirect evidence of planktonic food limitation of growth in the mollusc *Anadara granosa*. There is also evidence that some predator-free populations of *Mytilus edulis* are food limited (Kautsky 1982). Peterson (1982) found that high density depressed growth and reproductive effort of both *Protothaca staminea* and *Chione undatella*, two soft-bottom suspension feeders. In a related study, Peterson (1983) showed that individuals of *C. undatella* carrying the filter feeder *Crepidula onyx* grew slower than those free of this epibiont. Both intraspecific and interspecific effects on *Chione* growth were thought to be caused by competition for suspended food (Peterson 1982, 1983).

The experiments reported here were carried out to complement a study of vertical depletion of particulate organic matter (POM) over an intertidal mussel bed (Fréchette and Bourget 1985). They were designed to test the hypothesis that growth of individuals of a suspension feeder population was food limited due to suspended POM depletion in the benthic boundary layer (BBL).

Methods

The study was carried out at Pointe Mitis along the south shore of the St. Lawrence Estuary in 1980 and 1982. Bottom topography allowed the suspension of plastic cages containing "experimental" mussels 1.0 m above the mussel bed (0.5 kg flesh dry weight $\cdot m^{-2}$) so that their immersion time equalled that of control mussels in similar cages placed on the bottom. This experimental strategy is analogous to that used by Kautsky (1982). It allowed a test of food limitation without manipulating densities.

This experiment was carried out at two shore levels on 2 yr, midintertidal and upper to midintertidal in 1980 and lower and

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midintertidal in 1982. The experiment lasted 2 mo in 1980 (August and September) and 3 mo in 1982 (June, July, August). In 1980, 27 mussels were put in each of four cages. There were no replicates. In 1982, 20 cages were used, 5 for each treatment level. At each treatment level, 8–10 mussels 3.3–4.2 cm in length were placed in two of the cages (experiment I). The purpose of this part of the study was to assess the growth response of the local mussel population, since in the area of study, only larger mussels were abundant. In each of the three remaining cages, 23 mussels 1.0–4.5 cm in length were used (experiment II). This wider size range allowed a study of the response of mussels in terms of length–weight relationships. Length–weight regression coefficients can be interpreted as indices of condition of the mussels. Each year, all mussels were chosen from a single intertidal stock population, and it is assumed that at the beginning of each experiment, all mussels had a common length–weight relationship. Experimental lots were chosen so that the population size structure in all cages was similar. At the end of the experiments, total shell length was measured using a vernier caliper (±0.05 mm). Shell growth in experiment I was taken as the shell increment since the last annual growth ring. Flesh dry weight was measured after drying at 60°C for 72 h.

In September 1982, mussels were sampled from the crest and the sides of two intertidal hummocks (Barnes and Powell 1950; Seed 1969) and their length–weight relationships studied in order to test the hypothesis that mussels feeding higher in the BBL as a result of hummocking would be in better condition, since they would encounter more favorable growth conditions owing to vertical gradients in phytoplankton concentration. Mussels packed between hummocks were situated deeper within the BBL. However, they were not studied, since physical interference effects owing to their dense packing were more likely to occur and obscure the effect of vertical food gradients on their condition.

Results and Discussion

Growth

Dry weight and shell length increment were assessed in experiment I, 1982. Mussels from 1.0 m above the bottom tended to have greater flesh weight than control mussels lying on the bottom (Table 1). Shell length increment apparently was not influenced by growth conditions, except at low shore level, 1.0 m above the bottom, where growth appeared to be higher. The data were analyzed using a bivariate (flesh weight, length increment), two-way (height above the bottom, tidal level), nested (two replicates) ANOVA (GLM procedure, SAS) using replicate cages as the error term. Dry weights and length increments were normalized to shell length. Weight and shell length increment data were made homoscedastic ($P = 0.14$; BOXM, SPSS) using a square root transformation. Both shore level ($P = 0.025$) and height above the bottom ($P = 0.009$) influenced growth significantly (Table 2). There was no significant interaction between shore level and height above the bottom. To study the effect of growth conditions on weight and shell length increment separately, univariate ANOVAs were performed on each of these two variables (Table 3). Weight was influenced by shore level ($P < 0.01$) and height above the bottom ($P < 0.01$). The effect of height above the bottom ($P = 0.11$) and shore level ($P = 0.08$) on shell length increment was not significant. In both cases, the interaction term was not significant.

TABLE 1. Experiment I, 1982. Geometric means of dry weight and shell length increment of mussels grown on the bottom and 1.0 m above the bottom at low and midshore levels (data normalized for length).

Height above bottom (m)	Replicate	Weight		Length increment	
		Low	Mid	Low	Mid
0.0	1	0.124	0.093	0.059	0.085
	2	0.113	0.075	0.099	0.053
1.0	1	0.210	0.157	0.112	0.071
	2	0.196	0.133	0.207	0.068

TABLE 2. Experiment I, 1982. Effect of shore level and height above the bottom on flesh dry weight and length increment of mussels, as studied by two-way, nested, bivariate ANOVA procedures (square root transformed data).

Source of variation	Wilks' criterion	P
Shore level	$F(2,3) = 15.85$	0.025
Height above bottom	$F(2,3) = 32.80$	0.009
Interaction	$F(2,3) = 1.25$	0.404

TABLE 3. Experiment I, 1982. Effect of shore level and height above the bottom on flesh dry weight and shell length increment (in parentheses) studied by two-way, nested ANOVA procedures.

Source of variation	df	SS	F	P
Shore level	1	0,070	27,41	<0.01
	(1)	(0,116)	(5,33)	(0.08)
Height above bottom	1	0,172	67,49	<0.01
	(1)	(0,092)	(4,23)	(0.11)
Interaction	1	0,001	0,34	0.59
	(1)	(0,049)	(2,85)	(0.21)

Our results show that both shore level and height above the bottom affected mussel growth. Shore level has long been recognized as an important factor in controlling growth of blue mussels (Seed 1969). Of more immediate relevance to our experiments was the effect of height above the bottom. This effect tested the hypothesis that food depletion above the mussels (Fréchette and Bourget 1985) limited individual growth. Suspending mussels above the bottom indeed increased growth. This suggests that mussels were food limited. It is not clear, however, why flesh weight only was affected by height above the bottom. The effect of food concentration on shell growth may have been obscured by genetic differences between individuals (Freeman and Dickie 1979). Nonsignificant interaction terms indicate that growth was food limited at both shore levels. Hence, food limitation may be the norm rather than the exception for the population under study.

Transferring mussels 1.0 m above the bottom does not involve changes in POM concentration only. For instance, it is well known that current speed in boundary layers increases with height above the surface. In addition, there may be reduction in inorganic particulate matter concentration with height, as water in the immediate vicinity of suspension feeders may be charac-

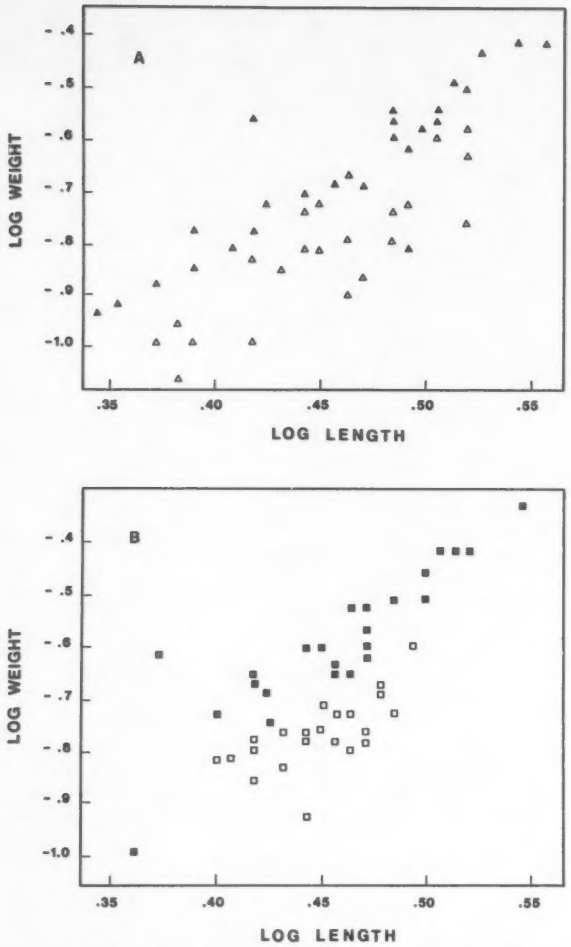

FIG. 1. Length–weight scatter plots for control (open symbols) and experimental (solid symbols) for (A) upper to midintertidal and (B) midintertidal levels, 1980 (log-transformed data).

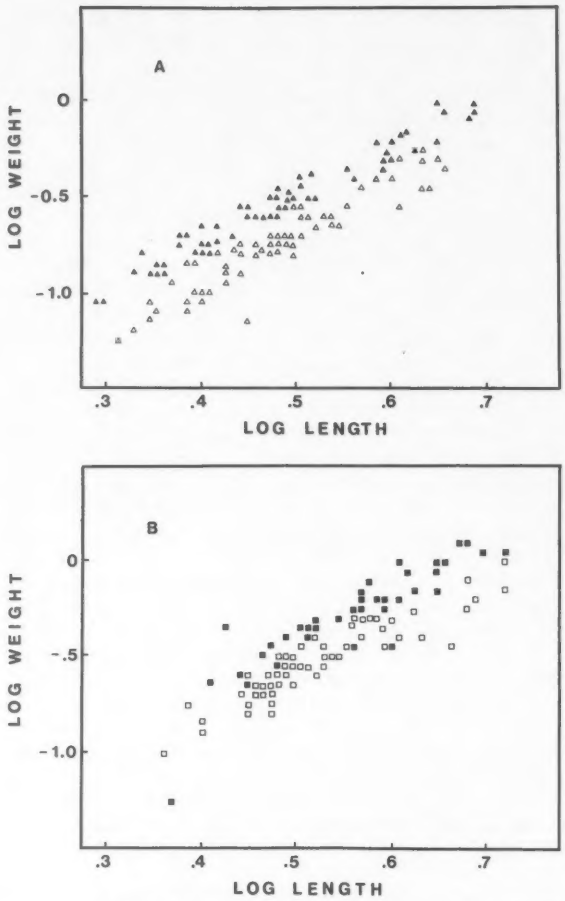

FIG. 2. Experiment II, 1982. Length–weight scatter plots for control (open symbols) and experimental (solid symbols) for (A) midintertidal and (B) low intertidal levels (replicates were pooled; log-transformed data).

terized by higher sediment concentration (Broom 1982). However, in our experiments, it is doubtful that current speed and sediment concentration differences accounted for growth enhancement at 1.0 m. On the one hand, Hildreth (1976) and Hildreth and Crisp (1976) have found no effect of water movement on filtration rate in *M. edulis*. On the other hand, it has been suggested that seston quality may be a key variable in controlling blue mussel annual growth dynamics (Bayne and Worrall 1980), poor seston quality leading to poor growth. However, laboratory experiments have shown that on a shorter time scale, the reverse trend may be observed. For instance, growth of *M. edulis* (Kiørboe et al. 1981) and *Spisula subtruncata* (Møhlenberg and Kiørboe 1981) was enhanced by sediment resuspension. Thus, it is possible that mussel growth at the bottom of the BBL was enhanced rather than reduced by higher resuspended material concentration. Therefore, we conclude that the lower growth of mussels at the bottom of the BBL was attributable to lower food availability, mainly phytoplankton.

Length–Weight Relationships

The response of mussels to feeding conditions was also studied by examining their length–weight relationships in two similar experiments (the 1980 experiment and experiment II, 1982). A logarithmic transformation of the data yielded linear relationships (Fig. 1A, 1B, 2A, 2B). Residual variances were homogeneous (F_{max}; Sokal and Rohlf 1981). The present data require that model II regressions be used instead of model I regressions (Ricker 1973; Laws and Archie 1981). However, statistical procedures presently available involve model I regressions (Ricker 1973; but see Clarke 1980). Therefore, model I and model II regressions must be examined when interpreting the results. Should strong discrepancies occur between model I and model II regression coefficients, then caution would be advised in interpreting the results of the statistical analyses. When ranked according to their magnitude, the order of regression coefficients and intercepts for each of the 1980 experiment and experiment II, 1982, do not change in model I and model II regressions (Table 4). Therefore, the results of

TABLE 4. Model I and model II regression equations for length (L) – weight (W) relationships of mussels in 1980 and in experiment II, 1982 (replicates pooled) (log-transformed data).

Experiment	Shore level	Height above bottom (m)	Model I	Model II
1980	Upper to midintertidal	0.0	$W = 2.47L - 1.92$	$W = 3.01L - 2.16$
		1.0	$W = 2.37L - 1.74$	$W = 2.63L - 1.86$
	Midintertidal	0.0	$W = 1.60L - 1.47$	$W = 2.42L - 1.84$
		1.0	$W = 2.68L - 1.81$	$W = 3.02L - 1.97$
1982	Midintertidal	0.0	$W = 2.62L - 2.00$	$W = 2.78L - 2.08$
		1.0	$W = 2.50L - 1.73$	$W = 2.56L - 1.76$
	Low intertidal	0.0	$W = 2.34L - 1.76$	$W = 2.53L - 1.85$
		1.0	$W = 2.73L - 1.81$	$W = 3.05L - 1.99$

TABLE 5. 1980 experiment. Test for homogeneity of slopes and ANCOVA on length–weight relationships of mussels (two-way design).

	Source	df	SS	F	P
Model	Model	7	1.946	64.17	<0.001
	Error	94	0.407		
	Total	101	2.353		
Test for homogeneity of slopes	Shore level	1	0.006	1.42	0.24
	Height above bottom	1	0.001	0.25	0.62
	Interaction	1	0.012	2.68	0.10
ANCOVA	Shore level	1	0.105	24.03	<0.001
	Height above bottom	1	0.487	111.85	<0.001
	Interaction	1	0.002	0.42	0.52
	Error	97	0.004		

TABLE 6. Experiment II, 1982. Test for homogeneity of slopes and ANCOVA on length–weight relationships of mussels (two-way, nested design; replicates used as error term).

	Source	df	SS	F	P
Model	Model	21	16.928	129.11	<0.001
	Error	193	1.205		
	Corrected total	214	18.133		
Test for homogeneity of slopes	Shore level	1	0.007	0.38	0.56
	Height above bottom	1	6.4×10^{-5}	0.00	0.95
	Interaction	1	0.064	3.61	0.10
ANCOVA	Shore level	1	0.266	12.60	<0.01
	Height above bottom	1	1.554	173.58	<0.001
	Interaction	1	0.066	3.12	0.12

regression and ANCOVA analyses apparently bear relevance for testing functional relationships (model II regression) in our experiments.

Regression coefficients were homogeneous in both experiments (Tables 5, 6). However, the ANCOVAs show that in both experiments, shore level and height above the bottom had significant effects on the length–weight relationships. For a given length, mussels lower on the shore and those 1.0 m above the bottom had a higher flesh content than their counterparts. The interaction terms were not significant. This indicates that all sizes were affected by food limitation, at both shore levels. These results are consistent with the hypothesis of emaciation in control mussels, as in experiment I, 1982.

Hummocking results in mussels being located at different levels within the BBL. Length–weight relationships for mussels from different parts of hummocks were not different (test of homogeneity of slopes, $P = 0.07$; ANCOVA, $P = 0.16$). According to the present data, therefore, it seems that position within hummocks does not result in differences in growing conditions, as long as trophic factors only are considered.

Competition for Food

There is growing direct and indirect evidence from field (Stiven and Kuenzler 1979; Broom 1982; Kautsky 1982; Peterson 1982, 1983) and experimental studies (Crisp 1960; Buss 1979; and probably also Buss and Jackson 1981) that growth of suspension feeders may be limited by food. Kautsky (1982) and Peterson (1982) observed that such growth limitation was accompanied by a negative effect on reproductive output, a criterion for competition (Begon and Mortimer 1981). Growth differences between experimental and control mussels resulted from vertical depletion of food, which is attributable to the feeding activity of the mussels themselves. Our results, therefore, are indicative of intraspecific competition for food in the mussel population.

Kautsky (1982) obtained results similar to ours in a study of a Baltic predator-free *M. edulis* population. However, competition is often enhanced in the absence of predators (Paine 1974). Therefore, the scope of Kautsky's results may be limited, since negligible predation is an infrequent and perhaps exceptional situation in sublittoral communities. The population studied at Pointe Mitis was located in the intertidal zone and was free from predators such as starfish (*Leptasterias polaris*), crabs (*Cancer irroratus*), and *Thais*. However, the population is subjected to other sources of mortality such as wave deportation, ice abrasion (Archambault and Bourget 1983; Gordon and Desplanque 1983), and cold temperatures (Bourget 1983). Eider ducks were also observed feeding on the mussels. Therefore, besides possible competition-induced death, there are other possible causes of mortality. This should result in alleviating competitive pressures. In spite of that, food depletion (Fréchette and Bourget 1985) and growth limitation were observed.

That food limitation can be alleviated and growth enhanced through the breakdown of vertical gradients in food by waves and currents (Fréchette and Bourget 1985) directly supports that part of the trophic group mutual exclusion hypothesis (Wildish and Kristmanson 1979) applicable to suspension feeders. Furthermore, the mutual interdependence of mussel consumption and growth and POM vertical depletion raises the possibility of some form of density dependence in summer mortality *M. edulis* mediated through the interaction of high temperatures and poor food availability (Incze et al. 1980).

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Organic Nitrogen Compounds in Atmospheric Precipitation: Their Chemistry and Availability to Phytoplankton

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Urea accounted for 30, 36, and 56%, respectively, of the water-soluble organic nitrogen (DON) compounds deposited from the atmosphere at two sites in New Zealand and one site in Japan. The other DON compounds were not identified but they were all of low molecular size, apparently anionic, and did not include detectable quantities of amino acids or uric acid. In axenic culture, *Chlorella* spp. grew successfully using DON from New Zealand precipitation as its only source of N; *Pediastrum biwae*, a phytoplankton endemic to Lake Biwa in Japan, also achieved successful growth using DON separated from Japanese precipitation. Ammonium-N and DON were deposited from the atmosphere in the absence of rain or snow, and we suggest that particulate matter, possibly soil, is a major source of these N compounds in atmospheric precipitation.

L'urée constituait respectivement 30, 36 et 56 % des composés d'azote organique solubles dans l'eau déposés de l'atmosphère (DON) à deux endroits en Nouvelle-Zélande et un au Japon. Les autres composés de DON n'ont pas été identifiés mais ils étaient tous de faible taille moléculaire, en apparence anioniques et ils ne contenaient pas de quantités décelables d'acides aminés ou d'acide urique. En culture axénique, on a obtenu une bonne croissance de *Chlorella* spp. sur du DON comme seule source de N, DON obtenu de précipitations néo-zéalandaises; *Pediastrum biwae*, un phytoplancton endémique au lac Biwa (Japon), a aussi bien poussé sur du DON déposé par les pluies. Des dépôts d'ammonium-N et de DON ont été précipités de l'atmosphère en l'absence de pluie ou de neige, ce qui porte à croire que la matière particulaire, peut-être le sol, est une importante source de ces composés azotés présents dans les précipitations atmosphériques.

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The presence of nitrate and ammonium in atmospheric precipitation is well known (Eriksson 1952; Uttormark 1974) but dissolved organic forms of nitrogen (DON) have received only sporadic attention. Most previous studies considered either total N or inorganic N but seldom both together, and only recently have estimates of DON concentrations in atmospheric precipitation become available. In many locations the atmospheric deposition rates of DON approach those of inorganic N (see Table 1), but despite this, few studies have considered the nature, origin, or ecological significance of the DON. Wilson (1959a, 1959b) found DON in snow from various locations in New Zealand and concluded that the DON originated from the surface of the ocean. Dean (1963) also studied precipitation in New Zealand, and reached similar conclusions. Sidle (1967) and Fonselius (1954) found amino acids in rain and Likens et al. (1983) detected primary amines at mean concentrations of 6 $\mu g\ C \cdot L^{-1}$ in wet-only precipitation from Ithaca, New York, and the Hubbard Brook Experimental Forest, New Hampshire, in the United States.

In a recent study near Lake Taupo, New Zealand, we found that DON was a high proportion of the total N in precipitation and that the annual average deposition rate of DON was 2.2 $kg \cdot ha^{-1} \cdot yr^{-1}$. This input is a substantial addition to the 3.6 $kg \cdot ha^{-1} \cdot yr^{-1}$ of inorganic N deposited by atmospheric precipitation on the lake surface (White and Downes 1977).

DON may contribute significantly to the N loads on other lakes of the world, as shown by the data in Table 1, and could be particularly important for lakes in which primary production is N limited. At present, however, the available data do not allow reliable assessments either of the spatial variability of DON deposition rates or its impact on lakes.

Our study was undertaken to elucidate the composition and origin of the DON and to establish its nutritional significance for phytoplankton.

Methods

Sample Collection

Precipitation was collected at three sites (Fig. 1), "Taupo 1" and "Taupo 2" in the catchment of Lake Taupo, New Zealand, and "Biwa" just outside the catchment of Lake Biwa, Japan.

TABLE 1. Deposition rates of inorganic and dissolved organic forms of N from the atmosphere.

Location		kg·ha^{-1}·yr^{-1} Inorganic	Organic	Reference
United States	Wisconsin	5.9	1.8	Kluesener 1972
		13.3	9.7	Kluesener 1972
		7.3	6.2	Hoeft 1971
	Florida	4.3	5.7	Hendry and Brezonik 1980
	Illinois	24.3	5.7	Kothandaraman and Evans 1978
	Minnesota	5.0	2.3	Verry and Timmons 1977
Canada	Ontario	10.1	4.4	Nicholls and Cox 1978
		7.8	3.2	Scheider et al. 1979
	Alberta	8.1	9.3	Caiazza et al. 1978
Sweden	Goteborg	10.2	1.3	Malmquist 1978
Venezuela	L. Valencia	3.8	1.3	Lewis 1981
South Africa	Durban	8.2	10.5	Simpson and Hemens 1978
Japan	L. Biwa	9.1	6.3	T. Kunimatsu, unpubl. data[a]
New Zealand	Taupo	0.25	2.2	This study (Taupo 1 sample)
		2.1	1.0	This study (Taupo 2 sample)

[a]Available from T. Kunimatsu, School of Agriculture, Shiga College, Kusatsu, Shiga 525, Japan.

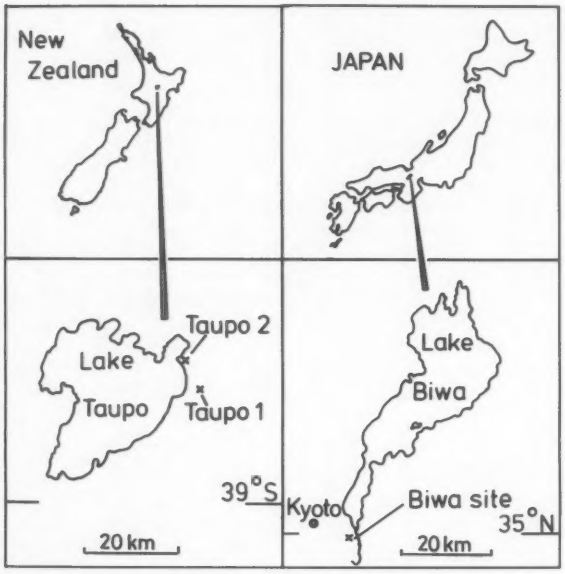

FIG. 1. Sites used in New Zealand and Japan for the collection of atmospheric precipitation.

The periods of sample collection were as follows: Taupo 1, 1 July 1981 – 30 July 1982; Taupo 2, 7 September 1983 – 18 November 1983; and for Biwa, 9 August 1983 – 24 September 1983. The apparatus was cleaned before use by soaking in HCl (approximately 5 mol·L^{-1}) for at least 24 h followed by rinsing and soaking in deionised water. This procedure eliminated the possibility of contamination from glass and plastic surfaces. Two plastic funnels (total area 0.08 m^2) covered with nylon mesh (0.5 mm) and plastic storage bottles were used for Taupo 1; Taupo 2 was collected with a curved glass sheet (area 0.5 m^2) and a glass storage bottle. At both sites the collecting surfaces were 1 m above ground level. There are few industrial emissions to the atmosphere in the Lake Taupo catchment. Accumulated precipitation was removed weekly to the laboratory and filtered (GF/C pore size approximately 1.2 μm). The Biwa sample was collected with four glass funnels (total area 0.28 m^2) and glass storage containers on the roof of a building at Shiga University, on the southern edge of the Lake Biwa catchment. The funnels were about 26 m above ground level and 2–3 km from ground of equivalent height. There were no obvious industrial emissions within a 2- to 3-km radius although the heavy industrial area of Osaka is to the south of the sampling site. Precipitation sampled at the Biwa site was collected and filtered (GF/C) within 12 h after each rainfall event.

Preservatives were not used in the sample collectors. Preliminary experiments showed that mercuric chloride, a very effective biocide, caused difficulties with column separations and chemical analyses. These problems were greatly enhanced after samples containing preservative had been concentrated. Other common preservatives (Galloway and Likens 1978) were expected to cause similar difficulties. During winter some samples remained at or below 0°C from the time they were deposited in the collectors, and DON in these samples was indistinguishable from DON collected at other times. We consider, therefore, that the lack of preservatives had little effect on the results of our study.

Following filtration, all samples were concentrated under vacuum at 40–50°C to approximately 5 mL and stored at −20°C. Analyses of the distillates showed that losses of DON during the concentration step were variable but always less than 20% of the total DON.

The sampling program at each location was terminated when a total of about 50 L of precipitation had been collected. The stored concentrates from a particular site were then combined and further concentrated. Thus, for each site, the total volume of precipitation collected was finally reduced to a single concentrate of approximately 5 mL. As the concentrates were frozen, a brown residue formed which was separated after thawing by filtration. These residues contained less than 5% of the total DON in the concentrates. The three filtrates, called Taupo 1, Taupo 2, and Biwa, were used for subsequent experiments.

After the major collection program had been completed at the Biwa site, material deposited in the funnels was sampled on a daily basis when practicable, between 12 December 1983 and 9 January 1984, irrespective of whether rain or snow had fallen.

Each time a sample was taken, the funnels were washed with deionised water and the sample was filtered (GF/C) and stored at −20°C for subsequent analysis.

The samples collected contained all the material deposited on the collectors. Our results and conclusions, therefore, relate to DON which is both dissolved in precipitation and readily leached by precipitation or deionised water from particulate matter in the atmosphere.

Analytical Methods

Nitrate-N + nitrite-N was analyzed by reduction to nitrite with hydrazine sulphate followed by colorimetric determination using sulfanilamide and *N*-1-naphthylethylene diamine dihydrochloride in both automated (Downes 1978) and manual procedures. The results of these analyses are referred to as nitrate-N. Analysis of ammonium-N was by the indophenol procedure, with an automated method adapted from Crooke and Simpson (1971) and a manual procedure using thymol and acetone (Koyama et al. 1976). For part of this study, total dissolved N was measured by an automated UV oxidation technique (Manny et al. 1971), and DON was estimated as the difference between total dissolved N and dissolved inorganic N (i.e. $NO_2 + NO_3 + NH_4$). Other estimates of DON were obtained from the difference between Kjeldahl-N and ammonium-N. Kjeldahl-N was measured by the manual ammonium-N procedure after digestion of the sample with sulphuric acid and hydrogen peroxide (Nicholls 1975).

Most DON measurements we report were obtained using the latter procedure, and for solutions from which ammonium-N had been removed by ion-exchange chromatography, DON was equal to Kjeldahl-N. Both the ammonium-N and Kjeldahl-N methods were optimised to measure up to 5 μg of N and had sensitivities of 6.5 μg N·absorbance^{-1}. The coefficients of variation for the Kjeldahl-N and ammonium-N determinations were both 9%; detection limits were 0.3 and 0.1 μg N, respectively.

Particulate N was determined by automated analysis of ammonium-N after digestion of the material retained on filters (GF/C) with a sulfuric acid – potassium persulfate – selenium – copper mixture (modified from Bremner 1965). The colorimetric procedure of Newell et al. (1967) and the enzyme procedure of McCarthy (1970) were used for urea-N analysis.

Column Chromatography

Sephadex G-25 was used for gel permeation chromatography with NaCl (0.05 mol·L^{-1}) as eluant. Biorad AG 50W-X12 with deionised water as eluant was used for cation-exchange chromatography. Columns were 200 × 20 mm ID. Recovery of DON from the columns was 100 ± 20%. The regeneration procedure used for the cation-exchange column between samples was as follows: (1) NaOH (0.01 mol·L^{-1}) to remove ammonium and adsorbed organic matter, (2) HCl (1 mol·L^{-1}) to remove NaOH, (3) NaCl (1 mol·L^{-1}) to convert the resin to Na form as shown by a return to neutral pH, and (4) deionised water to remove excess NaCl as monitored by conductivity.

Bioassays

Two bioassay experiments were performed to test the ability of phytoplankton to use DON isolated from precipitation as a source of nutrient N. DON in Taupo 1 was partially purified by chromatography on a column of Sephadex resin. The DON recovered from this column was then separated from both nitrate-N and ammonium-N by cation-exchange chromatography. The purified sample of DON concentrated to approximately 1 mL contained 167 μg DON, 0.16 μg NO_3-N, and less than 0.1 μg NH_4-N. An axenic culture (2 L) of *Chlorella* spp. (*ex* Lake Taupo) was established in Woods Hole MBL medium, pH 7.2 (Nichols 1973), in which the concentrations of P and N were both 100 μg·L^{-1}. When growth had slowed, aliquots (200 mL) of culture were transferred aseptically into each of three flasks. Phosphorus (25 μg P as K_2HPO_4) was added to each flask to eliminate the risk of P deficiency. Nitrate-N (200 μg) was added to one flask, the DON was added to a second flask, and the third was used as the control. Because of the small quantity of purified DON, 167 μg, replication of this experiment was not possible. It was necessary to confirm that growth was due to DON and not to some other constituent of the DON solution, and this was done by measuring the N contents of the phytoplankton at the end of the experiment. The reliability of these analyses was maximized by using a single DON treatment which ensured the largest possible difference between the phytoplankton N contents of treatment and control. The cultures were incubated at 16°C under fluorescent light (21 μE·m^{-2}·s^{-1}) with a 12 h light : 12 h dark cycle and continuous shaking.

At 18, 42, and 66 h after the introduction to the cultures of the N species, aliquots were removed aseptically from each flask for cell counts (in duplicate) using a haemacytometer and analysis of chlorophyll *a* (in triplicate). Chlorophyll was extracted in 90% acetone and analysed by fluorescence using an AMINCO SPF-500 spectrofluorometer calibrated with pure chlorophyll *a* (SIGMA Chemical Co., St. Louis, MO). After 66 h the phytoplankton were recovered by filtration (in triplicate for each flask) and analysed for particulate N.

Part of the DON in the Biwa sample was separated from both nitrate-N and ammonium-N by cation-exchange chromatography. This purified DON was used in bioassay experiments with *Pediastrum biwae* Negoro, a colony-forming phytoplankton endemic to Lake Biwa. About 1100 μg of DON free of inorganic N was obtained which allowed replicate flasks to be used for each time–treatment combination. Five forms of N, urea-N, uric acid-N, ammonium-N, nitrate-N, and DON from the Biwa sample, were tested using a set of 12 flasks (100 mL) for each form of N. Each flask contained 20 mL of sterile culture medium (Ishigama et al. 1982) to which was added 1 mL of axenic *Pediastrum* inoculum and 88 μg N contained in 1 mL of sterile solution to give a concentration in the flask of 4 μg N·mL^{-1}. The cultures were incubated at 20°C under continuous illumination of 100 μE·m^{-2}·s^{-1} with gentle shaking. At intervals of 72 h, colonies were counted in three flasks from each set.

Thin Layer Chromatography (TLC)

TLC on precoated silica G-60 (MERCK) plates was used to separate components of the DON from which nitrate-N and ammonium-N had been removed by cation-exchange chromatography. Two solvent systems were used: chloroform – methanol – formic acid, 3:1:1, and *n*-butanol – acetic acid – water 4:1:1. DON on the TLC plates was located by analysing areas (0.65 cm^2) of the coating for Kjeldahl-N. Ninhydrin was used to visualise urea and amino acids. Uric acid and other organic compounds were visualised with iodine vapour. The recovery of DON from the TLC plates varied between 70 and 130% of that applied due to background N on the plates and the cumulative errors of many Kjeldahl-N determinations.

Results

The volume-weighted average concentrations of nitrate-N, ammonium-N, DON, and total N in precipitation from the three sampling sites are given in Table 2. The much higher total N content of Biwa precipitation was mainly due to nitrate-N. The DON concentration at this site was approximately twice the average concentration at the Taupo sites.

Chromatography of Taupo 1, Taupo 2, and Biwa on columns of Sephadex resin gave the results shown in Fig. 2. The DON in each sample eluted from the column as one peak, and for all three samples this peak appeared at the same position relative to the column void volume. Since molecules with molecular weights greater than 5000 are excluded from this resin and elute at the void volume while smaller molecules elute subsequently, these results showed the DON compounds to be of low molecular size.

Cation-exchange chromatography resolved the DON from each of the three samples into two peaks as shown in Fig. 3. For Taupo 2 and Biwa the first peaks eluted at the position expected for anions, cf. the nitrate peak, but for Taupo 1 the first DON peak eluted just after nitrate-N. The second peaks of DON appeared at the same elution volume for all three samples. This result indicated the presence of similar DON compounds in all samples and also showed that these compounds had neutral charge. Urea is a low molecular weight, zero charged DON compound commonly found in nature, and analysis by the method of Newell et al. (1967) confirmed that the second DON peaks in all three samples were mostly urea (Fig. 3). For each sample the fractions containing the second peak of DON were combined and analysed more accurately for both urea-N by the enzyme method and Kjeldahl-N. As a percentage of the total DON in precipitation, urea-N was 36, 30, and 56% for Taupo 1, Taupo 2, and Biwa, respectively. The nonurea-N in the second peaks is believed to be DON tailed from the first peaks.

Analyses using the method of Newell et al. (1967) detected a small amount of urea-N in the first DON peaks eluted from the cation-exchange column (Fig. 3). Urea is unlikely to elute from the column at this position, but another DON compound may have decomposed to urea during the analysis or interfered directly. Tests with glycine and acetamide confirmed that these two compounds do not give positive results in the urea analysis of Newell et al. (1967), but uric acid, a purine produced by N metabolism in animals, gave a urea-N reaction equivalent to 10% of the amount of uric acid-N present. Uric acid is a low molecular weight anion as are the DON compounds in the first peaks eluted from the cation-exchange column.

The DON compounds in the first peaks of Taupo 2 and Biwa were examined further by TLC. Urea and uric acid were both mobile in a chloroform – methanol – formic acid solvent, but most of the DON in both samples remained on the origin (Fig. 4A). The possible presence of amino acids, many of which are anionic, was examined using an *n*-butanol – acetic acid – water solvent in which all common amino acids are mobile (Stahl 1969). The DON in both samples migrated to positions typical of amino acids, cf. the position of glycine ((Fig. 4B), but none of the DON gave a positive reaction with ninhydrin, a reagent capable of detecting most amino acids in nanogram quantities.

The DON used in the bioassay experiments was that which was obtained free of nitrate-N from the cation-exchange column (Fig. 3), i.e. elution volume 30–70 mL for Taupo 1 and 40–70 mL for Biwa. The growth of *Chlorella* spp. using DON from Taupo 1 as its sole source of N was similar to the growth

TABLE 2. Volume-weighted average concentrations ($\mu g\ N \cdot L^{-1}$) of N species in atmospheric precipitation at the three sampling sites.

Form of N	Site and period of sampling		
	Taupo 1 (1 July 1981 – 30 July 1982)	Taupo 2 (6 May 1983 – 26 Oct. 1983)	Biwa (9 Aug. 1983 – 24 Sept. 1983)
NO_3-N	11	48	665
NH_4-N	10	130	346
DON	162	81	236
Total N	183	259	1247

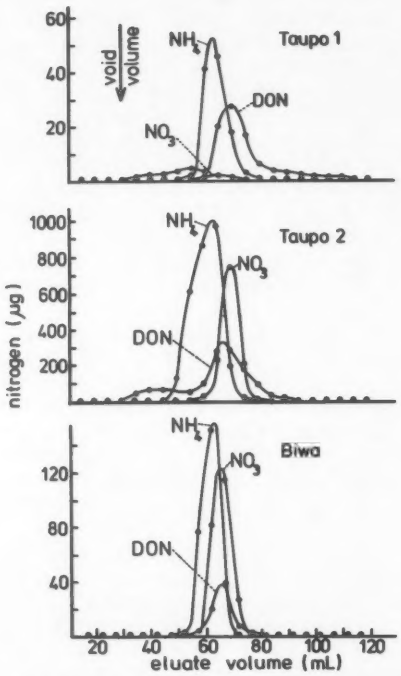

FIG. 2. Elution patterns of ammonium-N, nitrate-N, and DON from column chromatography of the precipitation concentrates on Sephadex G-25 with NaCl ($0.05\ mol \cdot L^{-1}$) as eluant.

achieved by this phytoplankton using nitrate-N (Fig. 5A). The N-treated cultures showed a 5- to 10-fold increase over the control culture in both cell numbers and chlorophyll *a* concentrations. At the end of the incubation period the phytoplankton in the N-treated cultures contained 90 and 95%, respectively, of the added nitrate-N and DON. Over a period of 12 d, *P. biwae* increased its number of colonies by a factor of 5 using DON separated from the Biwa sample as its sole source of N. Compared with the results for DON, the growth of this phytoplankton was greater using nitrate-N, ammonium-N, and uric acid-N and slightly less using urea-N.

The deposition rates of ammonium-N, total DON, and urea-N from dry fallout and wet precipitation at the Biwa sample site are given in Table 3. Substantial quantities of these N forms were deposited with dry fallout and although, in general, the deposition rates were higher for periods which included rain or snow, on two occasions the deposition rates during dry periods were of

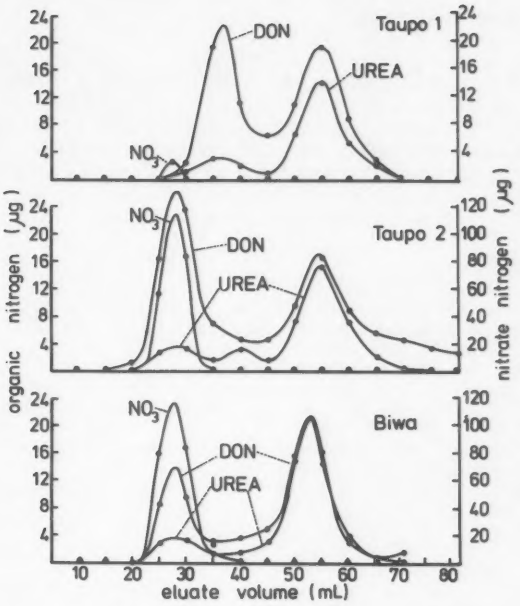

FIG. 3. Nitrate-N, total DON, and urea-N in eluate fractions from cation-exchange chromatography of the three precipitation concentrates. The resin was Biorad AG 50W-X12 cation-exchange (Na form) and was eluted with deionised water.

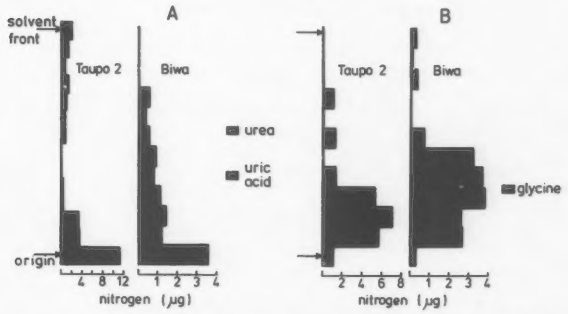

FIG. 4. Distribution of Kjeldahl-N on TLC plates (Merck Silica G-60) after chromatography of DON in the first peaks eluted from the cation-exchange column (see Fig. 3). The positions of pure urea, uric acid, and glycine when chromatographed simultaneously with the DON are shown. (A) Chloroform – methanol – formic acid, 3:1:1; (B) *n*-butanol – acetic acid – water, 4:1:1.

similar magnitude to those during wet precipitation. Precipitation fell as snow three times and these samples remained frozen until collection. The amounts of urea in these samples were similar to those found in samples of precipitation collected at other times.

Discussion

Our results show that in both Japan and New Zealand, the water-soluble organic N compounds deposited from the atmosphere with rain, snow, and particulate matter include urea and low molecular weight organic anions. Since urea is deposited from the atmosphere in both countries, it probably has a natural

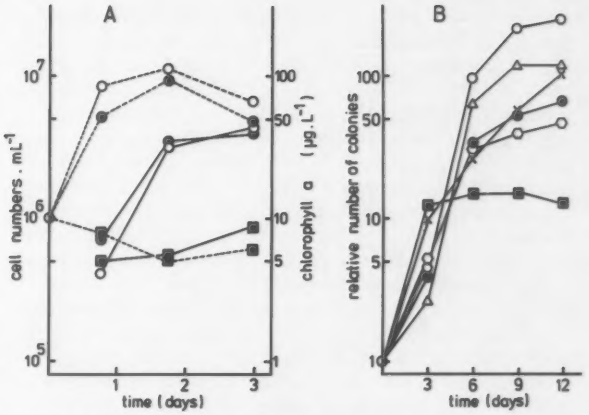

FIG. 5. Growth responses of phytoplankton to various forms of N added to axenic, N-deficient cultures. (A) *Chlorella* sp.: DON was separated from the Taupo 1 precipitation concentrate; (B) *P. biwae*: DON was separated from precipitation collected at the Biwa site. ●, DON from atmospheric precipitation; ○, nitrate-N; △, ammonium-N; ×, uric acid-N; ◯, urea-N; ■, control; —, cell numbers (Fig. 5A) or relative number of colonies (Fig. 5B); ---, chlorophyll *a* (Fig. 5A).

TABLE 3. Deposition rates ($\mu g \cdot h^{-1}$) of inorganic and organic forms of N at the Biwa sampling site.

Period of sample accumulation (h)	Precipitation (mm)	NH_4-N	Total DON	Urea-N
47	3.4	19.3	2.40	1.90
48	0	5.92	1.38	0.34
29	0	3.76	0.55	0.44
51	0	5.02	1.02	0.30
90	5.0	7.16	3.38	1.05
23	0	19.7	8.52	3.05
25 (snow)	6.7	36.5	9.66	6.38
24	0	6.05	1.15	0.28
74 (snow)	0.7	17.1	5.57	1.57
24 (snow)	3.7	21.6	3.85	2.92
27	0	3.86	0.56	0.38
22	0	12.7	4.18	3.67
24	0	7.36	2.98	0.63

origin. Birds and insects are undoubtedly contributors of DON to the atmosphere by their excretion of uric acid (Campbell and Goldstein 1972; Stryer 1975), but this compound was not a significant component of the DON in our study. Although uric acid can be degraded to urea by bacteria (Neilson and Larsson 1980), the snow we collected and maintained at 0°C, thus reducing bacterial activity, contained urea. We conclude that winged animals are not major contributors of DON to the atmosphere.

Urea, the primary excretion product of animals, is ubiquitous on land surfaces. On the surfaces of lakes and oceans the organic compounds produced by plankton excretion and decomposition (Garrett 1967; Nishizawa 1971; Williams 1967; Carlson 1983; van Vleet and Williams 1983) include urea (Remsen 1971; Saijo et al. 1974). Urea is therefore widespread on land and water surfaces, and since it has a low molecular weight (60.06), boils at 132.7°C, and has neutral charge at the pH of natural ecosystems, it is more volatile than other common organic N compounds such as amino acids. Direct volatilization from land and

water surfaces is therefore a likely mechanism for the introduction of urea into the atmosphere. Aerosols from ocean surfaces may also transport organic compounds into the atmosphere (Wilson 1959a, 1959b; Gershey 1983). However, there is another possible transfer mechanism. We found that even in the absence of wet precipitation, DON and ammonium-N were deposited in the sample collectors. Under these conditions the predominant material deposited is particulate matter, and since it contained ammonium-N and DON, including urea, we suggest that soil could be the major component of this particulate matter. The flocculant residue that formed in the sample concentrates during freezing contained low concentrations of N, was brown, and dissolved readily in alkali, properties that are characteristic of soil humic matter. Humic matter is a high molecular weight polymer with low volatility and its appearance in atmospheric precipitation would be consistent with the aerial transport of soil particles. In their study of organic carbon in precipitation, Likens et al. (1983) also considered soil to be a probable source.

The other DON compounds in precipitation were not identified. In the first fractions from the cation-exchange column, the DON was accompanied by brown organic material, and TLC with a variety of different solvents failed to separate the brown material from the DON. If DON is carried into the atmosphere on soil particles, then the anionic DON found in our study may be N-containing "fulvic" acids. Although the DON did not contain uric acid or ninhydrin-positive compounds (i.e. amino acids and peptides) in detectable quantities, the absence of other purines or pyrimidine bases was not confirmed. These results do not conflict with previous reports of amino acids in precipitation because the concentrations reported were low, e.g. the total concentration of amino acid-N found by Sidle (1967) was about 7 $\mu g \cdot L^{-1}$. Our limit of detection for amino acid-N on the TLC plates was equivalent to 1 $\mu g \cdot L^{-1}$ in the original precipitation.

Despite the lack of flask replication in the bioassay with *Chlorella* spp., the magnitude of the growth response with DON as sole N source and the almost complete incorporation of DON into the cells is evidence that DON in precipitation over the Lake Taupo catchment is a directly available source of N for lake water phytoplankton. From the bioassay using *P. biwae*, we conclude that at least 50% of the DON falling over the Lake Biwa catchment is also directly available to phytoplankton. These bioassay results were not surprising, since phytoplankton can grow using many low molecular weight N-containing compounds. The utilisation of urea-N by phytoplankton is well known in lakes (Saijo et al. 1982) and oceans (Eppley et al. 1971; McCarthy 1972; Mitamura and Saijo 1975; Fisher and Cowdell 1982). Other compounds, some of which are anionic at the pH of natural waters, are also potential sources of N for phytoplankton (Ammann and Lynch 1964; Belmont and Miller 1965; Hellebust and Guillard 1967; Liu and Hellebust 1974). In our study, uric acid was used by *P. biwae* for growth, and similar results with other plankton have been reported for this compound and for other purines and purine derivatives such as hypoxanthine, xanthine, and allantoin (van Baalen and Marler 1963; Antia et al. 1975, 1980; Fisher and Cowdell 1982; Devi Prasad 1983).

We conclude that DON in precipitation must be considered as a readily available source of N for phytoplankton. From the data in Table 1 we suggest that this additional load of "available" N could be a substantial proportion of the total N load on lakes from atmospheric precipitation.

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Predicting the Vertical Distribution of Fish Populations: Analysis of Cisco, *Coregonus artedii*, and Yellow Perch, *Perca flavescens*

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Rudstam, L. G., and J. J. Magnuson. 1985. Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. 42: 1178–1188.

We develop a model based on fish behavior in temperature and oxygen gradients that yields quantitative predictions of the vertical distribution of a fish population throughout the water column. The model was tested against observed vertical distributions of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*, in 1981 and 1982 from five Wisconsin lakes. In some cases, the model seemed adequate for cisco, but in most cases, they occupied a temperature lower than their final preferendum. Occupation of lower temperature is consistent with a response to less than ad libitum food rations expected in these oligotrophic to mesotrophic lakes. In Lake Mendota, which is eutrophic with an anaerobic hypolimnion, cisco occupied temperatures higher than predicted by the model. For perch distributions, avoidance of high light intensities appears important. We did not observe effects of interspecific segregation between cisco and perch in their vertical distributions beyond that expected from differences in their preferred temperatures. Deviations of actual distributions from predictions of our relatively simplistic two-factor model can be used to help identify and evaluate other important physical and biotic factors influencing vertical distributions.

Les auteurs ont élaboré un modèle basé sur le comportement du poisson selon des gradients de température et d'oxygène; ce modèle fournit des predictions quantitatives de la répartition verticale d'une population dans toute la colonne d'eau. Il a été essayé par rapport à des répartitions verticales du cisco (*Coregonus artedii*) et de la perchaude (*Perca flavescens*) observée en 1981 et 1982 dans cinq lacs du Wisconsin. Dans certains cas, le modèle semblait adéquat pour le cisco mais le plus souvent, cette espèce recherchait des températures inférieures à celles qu'elle préférait finalement. Ce phénomène correspond à la réaction aux quantitiés moindres de nourriture que ces lacs oligotrophes et mésotrophes sont censés offrir. Dans le lac Mendota, lac eutrophe où l'hypolimnion est anaérobie, le cisco recherchait des températures supérieures à celles prédites par le modèle. La répartition de la perchaude semblait être liée à son évitement des fortes intensités lumineuses. Les auteurs n'ont pas observé d'incidences de ségrégation interspécifique entre le cisco et la perchaude dans leur répartition verticale au-delà prévue en fonction des différences des températures recherchées. Les écarts entre les répartitions réelles et les prédictions du modèle bifactoriel relativement simple peuvent servir à déterminer et à évaluer d'autres importants facteurs physiques et biotiques qui influent sur les répartitions verticales.

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Pelagic fishes generally do not occupy the entire water column. Their restricted vertical distributions may be related to a number of factors, such as temperature, oxygen, light, interactions with other species, and prey availability. Vertical gradients in temperature and oxygen concentrations occur in lakes during summer stratification. Fish distributions are often correlated with these gradients (e.g. Juday and Wagner 1908; Fry 1937; Frey 1955; Hasler and Tibbles 1970; Valtonen 1970; Brandt et al. 1981). In this paper we develop a model that yields quantitative predictions of the vertical distribution of a fish population throughout the water column based on known responses to temperature and oxygen. Such predictions can be considered a null hypothesis stating that fish vertical distribution is dependent only on temperature and oxygen concentrations. We tested this hypothesis by comparing observed and predicted vertical distributions of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*, in five Wisconsin lakes, where the pelagic assemblages are dominated by one or both of these species. Deviations from predictions provide insights about the importance of other factors not included in the model, such as light and inter- and intra-specific interactions.

Our model assumes that fish are distributed around their species-specific final preferendum — the temperature ultimately selected in the laboratory regardless of prior thermal history (Fry 1947, 1971; Magnuson et al. 1979; Reynolds and Casterlin 1979a). Neill and Magnuson (1974) found close agreement between laboratory-determined final preferenda and temperatures occupied by four species of centrachids in a thermal

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outfall. However, fish are sometimes found in temperatures lower than their laboratory-determined final preferendum. Ferguson (1958) suggested that this difference between laboratory measurements and field observations is the result of inappropriate comparisons. Larger fish typically observed in lakes may have a preferred temperature lower than the smaller fish normally used in experiments. Yellow perch, for example, show such an ontogenetic shift (McCauley and Read 1973). Alternatively, fish may deliberately choose a lower temperature than their final preferendum to maximize growth rates (Brett 1971, 1979; Biette and Geen 1980). Laboratory experiments indicate that some species may choose a lower temperature when fed restricted rations (Stuntz and Magnuson 1976; Javaid and Anderson 1967; Reynolds and Casterlin 1979b). This suggests that temperature preference can be dependent on food availability (Crowder and Magnuson 1983).

Fish may also be forced by other factors, such as high light intensities, social interactions, and prey availability, to occupy temperatures outside their preferred range (see review by Magnuson and Beitinger 1978). We have attempted to include one such factor, low oxygen concentrations, in the model.

If deviations from model predictions result from the fish actually choosing a lower temperature owing to lower food availability or to ontogenetic shifts in preference, we would expect that a model based on a "preference temperature" lower than the final preferendum would give close fit to the observed distributions. However, there is no reason to expect a good fit if factors other than temperature and oxygen are important.

Model Derivation and Calculations

We obtained distributions of time spent by single yellow perch and cisco in different temperature and oxygen concentrations from laboratory experiments reported in the literature. These distributions can be considered response functions to temperature and oxygen. The product of the two functions forms a response surface where the z-axis represents the relative amount of time a fish would spend in a particular temperature–oxygen combination. For example, in Fig. 1, the z-value is 1 at 12°C and 6 mg/L and 0.5 at 12°C and 3.2 mg/L. The fish would then spend twice as much time at 12°C and 6 mg/L as compared with 12°C and 3.2 mg/L.

Shape of Response Functions

Temperature

Magnuson et al. (1979), analyzing data from laboratory experiments by several authors, found that the time spent by fish in different temperatures could be approximated by a normal curve with a mean at the preferred temperature and a standard deviation of 2°C. These curves fit data from several fish species with different preferred temperatures including yellow perch (McCauley and Read 1973) and arctic cisco, *Coregonus autumnalis* (Fechhelm et al. 1983), and were therefore used here as temperature response functions for both cisco and yellow perch. Skewed preference curves as suggested by Reynolds and Casterlin (1976) and Dewitt and Friedman (1979) were not used in our model.

Oxygen

The oxygen response function was assumed to be linear between lower and upper threshold concentrations. The fish were assumed to completely avoid concentrations below the lower threshold and to be unaffected by concentrations above

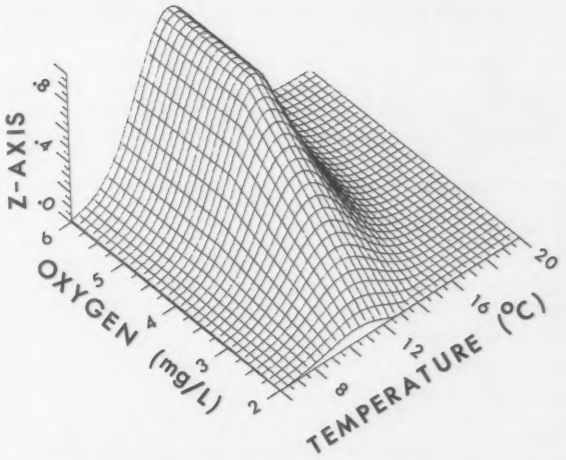

FIG. 1. Response surface towards oxygen and temperature calculated for cisco. The z-axis represents the amount of time a fish would spend in a particular temperature and oxygen concentration relative to the time it would spend at its most preferred temperature–oxygen combination (where $z = 1$). See text for explanations.

the upper threshold. This shape of the oxygen response function is supported by Whitmore et al.'s (1960) experiments on chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *Oncorhynchus kisutch*. It also corresponds to Brett's (1979) interpretation of data, primarily from Herrmann et al. (1962, coho salmon) and Stewart et al. (1967, largemouth bass *Micropterus salmoides*), on the effect of oxygen on growth. We assumed that the lower threshold corresponds to the lethal concentration and the upper threshold to the highest concentration at which an avoidance reaction or a negative effect on growth can be detected (the incipient sublethal threshold of Davis 1975).

Available information on the interaction between temperature and oxygen responses is difficult to interpret. Comparisons of different investigations are generally not practical because of the variety of techniques used (Doudoroff and Shumway 1970; Brett 1979). Even studies where the effect of temperature on lethal oxygen concentrations was the main objective have not given consistent results (see review by Doudoroff and Shumway 1970). The variety of mechanisms fish use to increase their oxygen uptake at low concentrations, e.g. faster ventilation rates, lower venous oxygen tensions, increased stroke volume, and increased functional area of the gills (Randall 1970), complicates the interaction. However, to consider responses to oxygen independent of temperature would be contrary to our current understanding of fish bioenergetics (Kitchell et al. 1977; Brett 1979; Brett and Groves 1979; Crowder and Magnuson 1983). As a first approximation, we assumed that the lower threshold concentration increases with temperature at the same rate as standard metabolism. We believe that this is a reasonable assumption because, at lethal concentrations, the oxygen uptake rate should be sufficient only for maintaining standard metabolism and the fish should be using all mechanisms available for increased oxygen uptake at maximum capacity. Thus, the oxygen uptake rate should be directly proportional to ambient oxygen levels. The upper threshold may or may not be temperature dependent. Whitmore et al. (1960) found temperature to be the main variable responsible for differences in oxygen avoid-

ance reactions for coho and chinook salmon both within and between seasons. With yellow perch, however, Petit (1973) did not observe any difference in the oxygen concentrations at which the first sign of stress (defined as increased opercular movement) occurred at 15 and 22°C. We followed Whitmore et al. (1960) for the confamilial cisco and Petit (1973) for the perch.

To summarize, the model consists of the following equations:

$$(1)\quad F(T, Ox) = f(T)\cdot g(Ox, T)$$

where F is the combined response function, f is the temperature response function, g is the oxygen response function, T is temperature (degrees Celsius), and Ox is oxygen concentrations (milligrams per litre);

$$(2)\quad f(T) = \frac{1}{S\sqrt{2\pi}}\cdot e^{\frac{-(T-T_p)^2}{2S^2}}$$

where S is the standard deviation and T_p is the preferred temperature;

$$(3)\quad g(Ox, T) = \begin{cases} g = 0 & \text{for } Ox < L(T) \\ g = a + bOx & \text{for } L(T) < Ox < A(T) \\ g = 1 & \text{for } Ox > A(T) \end{cases}$$

where $L(T)$ is the lethal oxygen level as a function of temperature (lower threshold), $A(T)$ is avoidance oxygen level as a function of temperature (upper threshold), and a and b are constants calculated so as to give a linear function between the points $(L(T), 0)$ and $(A(T), 1)$. An example of a combined temperature–oxygen response surface calculated for cisco is presented in Fig. 1.

Predicting Vertical Distributions

To calculate the number of fish expected at each metre of depth in a lake, we need a probability density function (PDF) of the time spent by single fish at different depths. This PDF is obtained by (1) calculating the value of the response surface at each metre of depth corresponding to measured temperatures and oxygen levels and (2) standardizing these values so their sum over all depths equals 1 (the probability of finding the fish somewhere should equal 1). This PDF also represents the vertical distributions of a population if we assume that each fish in the population behaves independently. Thus, the model does not consider any intraspecific interactions. The number of fish expected at a given 1-m depth interval, then, equals the total number of fish in a population or sample multiplied by the proportion of fish expected at that depth.

Parameter Estimations

Temperature

Laboratory experiments on temperature preferences of coregonines are rare. For cisco, the upper limit of their voluntarily occupied temperature range can be estimated at 17°C (Cahn 1927). Cahn slowly heated one end of a large tank and observed which temperature ciscoes avoided. This corresponds to a preferred temperature of 12°C if cisco have a temperature response similar to several other fish species, including the confamilial rainbow trout, *Salmo gairdneri* (avoidance temperature approximately 5° higher than preferred temperature) (McCauley and Pond 1971; Magnuson et al. 1979). Final preferenda of juvenile arctic cisco were estimated to 13.5°C at 30‰ salinity and 15.6°C at 15‰ (Fechhelm et al. 1983). From their table 1, the final preferendum at 5‰ (the lowest salinity tested) can be estimated to 14°C. For lake whitefish, *Coregonus clupeaformis*, preferred temperatures of 12.7°C (2-yr-olds, F. T. Tompkins and J. M. Fraser, manuscr., cited in Ferguson 1958) and 10°C (fingerlings, Opuszynski 1974) have been reported. However, Coutant (1977) and Jobling (1981) listed no salmonid species with a laboratory-determined preferred temperature lower than 11.7°C. We believe 12°C to be a reasonable estimate of the final preferendum for cisco.

There are several laboratory investigations on the temperature preference of yellow perch. The final preferendum during the summer appears to depend on the size of the fish (McCauley and Read 1973). Reported values range from 21.4 to 24.2°C for YOY (Neill and Magnuson 1974; McCauley and Read 1973; Cherry et al. 1977) and from 20 to 21°C for older fish (Ferguson 1958; McCauley and Read 1973; Reutter and Herdendorf 1974; Reynolds and Casterlin 1979b), although higher values (25–27°C) have also been reported (Barans and Tubb 1973). Since the perch caught in gill nets were 1+ and older, we used 21°C as an estimate of their preferred temperature.

Oxygen

Lethal oxygen levels have been determined for a number of Eurasian coregonines (Privolnev and Koroleva 1953; Privolnev 1954; Streltsova et al. 1964; Chernikova 1964), but not for cisco. We used the mean value from these studies, 1.9 mg/L (SD = 0.21, N = 15, range 1.0–3.8, temperatures 10–15°C). We assumed this value for 12°C and considered the lethal concentration to vary with temperature as the standard metabolism of a generalized salmonid (Table 1) (Stewart 1980). This corresponds to a Q_{10} value of 2.0. If we further assume that the upper threshold is 2.5 mg/L higher than the lower threshold, we obtain for cisco threshold values of 1.9 and 4.4 mg/L at 12°C and 3.5 and 6.0 mg/L at 20°C. These upper threshold levels correspond to observations by Whitmore et al. (1960) on chinook salmon. The salmon did not avoid oxygen concentrations above 4.5 mg/L at 12°C and above 6.0 mg/L at 20°C. Davis (1975) calculated a mean value of 6.0 mg/L for the incipient limiting concentrations (SD = 0.42, range 3.21–8.09) from 19 studies on freshwater salmonids. These studies did not include any coregonines and were conducted at different temperatures and with varying criteria for detecting effects of low oxygen concentration. However, the numbers indicate that our assumptions are reasonable.

The mean lethal oxygen level for yellow perch and the physiologically and ecologically similar Eurasian perch, *Perca fluviatilis* (Thorpe 1977), from eight laboratory studies was 0.76 mg/L (SD = 0.42, N = 8, range 0.3–1.4, temperatures 0–27°C) (Doudoroff and Shumway 1970). We assumed that the lethal concentration is 0.8 mg/L at 15°C (the mean of the temperatures used in these studies) and has the same dependency on temperature as standard metabolism (Kitchell et al. 1977). This corresponds to a Q_{10} value of 2.3. In a study of the responses of yellow perch to low oxygen concentrations, Petit (1973) observed signs of stress (defined as increased opercular movements) at concentrations of 5 mg/L at both 15 and 22°C. No temperature effect was apparent. We therefore assumed the avoidance level to be 5 mg/L and independent of temperature. The parameter values are summarized in Table 1.

Study Area

Four of the five study lakes are located in Wisconsin's Northern Highland Lake District — Big Muskellunge, Crystal,

TABLE 1. Parameter values used in the vertical distribution models for cisco and yellow perch (see text for sources).

Parameter	Symbol	Equation	Cisco	Perch
Preferred temperature (°C)	T_p	2	12	21
Standard deviation (°C)	S	2	2	2
Lower oxygen threshold (mg/L)	$L(T)$	3	$0.84e^{0.068T}$	$0.25e^{0.074T}$
$L(T)$ at T_p (mg/L)			1.9	1.2
Upper oxygen threshold (mg/L)	$A(T)$	3	$L(T) + 2.5$	5.0

TABLE 2. Morphometric and limnological characteristics of the lakes investigated. Sources: LTER – Northern Lakes Project and Poff and Threinen (1962).

Lake	Water source[a]	Area (ha)	Max. depth (m)	Mean depth (m)	Alkalinity (mmol/L)	Conduct. (μS/cm at 20°C)	pH
Sparkling	S	81	20.0	11.3	0.61	74	7.9
Big Muskellunge	S	396	21.4	7.0	0.39	48	8.2
Trout	D	1605	35.7	13.8	0.82	90	8.3
Crystal	S	37	20.4	10.4	0.10	13	6.1
Mendota	D	3983	25.0	12.2	1.40	281	8.7

[a]S = seepage lake; D = drainage lake.

Sparkling, and Trout lakes. They are surrounded by conifer and aspen–birch forests and are all within 5 km of the Trout Lake Station of the University of Wisconsin-Madison (46.0°N, 89.7°W) (Magnuson and Frost 1982). Lake Mendota is in south-central Wisconsin (43.1°N, 89.4°W). Morphometric and limnological characteristics of the five lakes are summarized in Table 2.

Methods

Field Sampling

Five lakes were sampled between July 31 and August 24, 1981, and four between July 27 and August 19, 1982. Seven vertical gill nets were used, each with a different mesh size (19-, 32-, 38-, 51-, 64-, and 89-mm stretch mesh in both years, with a 127-mm net in 1981 and a 25-mm net in 1982). The nets, 4 m wide and 18 m deep, were made of multifilament nylon twine and mounted on foam rollers following the description by Kohler et al. (1979). The seven vertical nets were sex next to each other in a straight line along the 18-m depth contour for 48 h per lake. In 1981, Trout Lake was fished for an additional 24 h with the nets suspended from the surface (32- and 38-mm mesh) or from 13 m (19-, 51-, 64-, and 89-mm mesh) to 27 m depth, after a large number of fish targets were observed on sonar in water deeper than 18 m. In 1982 the nets were elongated by attaching additional webbing to allow fishing with all mesh sizes from the surface to 30 m depth. The nets were checked approximately every 6 h in 1981, between 03:00 and 05:00, 09:00 and 11:00, 15:00 and 17:00 and 21:00 and 23:00 central standard time, and once every 24 h in 1982. All fish caught were identified; total lengths were measured to the nearest millimetre and depths of catch noted in 1-m intervals.

Temperature and oxygen profiles were taken every second and fourth week, respectively, by the Long Term Ecological Research – Northern Lakes project. Linear interpolation between sampling dates surrounding the times of fish sampling was used to estimate vertical profiles of temperature and dissolved oxygen (Fig. 2).

Calculations

The observed vertical distributions of cisco and yellow perch were compared with predictions from the model described above using a Kolmogorov–Smirnov test (Sokal and Rohlf 1969). Day and night distributions, when significantly different, and distributions of different size classes were analyzed separately. We did this because diel vertical migrations have been reported for yellow perch (e.g. Hasler and Bardach 1949; Hasler and Villemonte 1953) and for coregonines (e.g. Northcote and Rundberg 1970; Dembinski 1971; Nilsson 1979; Enderlein 1982). Also, different size classes may segregate spatially (Fry 1937; Ferguson 1958; Valtonen 1970; Brandt 1980), possibly as a response to different temperature preferences (Ferguson 1958; McCauley and Huggins 1979).

Results

At least 87% of the catch in the gill nets in both years and all lakes consisted of yellow perch and cisco (Table 3). No perch were caught in Sparkling Lake, although it occurs there (pers. obs.), and no cisco were caught in Crystal Lake. In 1981, cisco were primarily caught from dusk to dawn, and perch were caught, with the exception of Crystal Lake, from dawn to dusk. The perch in Crystal Lake were found close to the bottom during the day and throughout the epilimnion at night. In the other lakes, diel vertical migrations either did not occur or were not detectable due to low catches in gill nets during the day (cisco) or during the night (perch) and uncertain interpretations of sonar charts (Rudstam 1983). Horizontal diel migrations may occur (Engel and Magnuson 1976; L. G. Rudstam, pers. obs.). Sonar charts revealed the same pattern in 1982.

Different year classes of cisco had different depth distributions in 1981 in Trout and Sparkling lakes, but not in Big

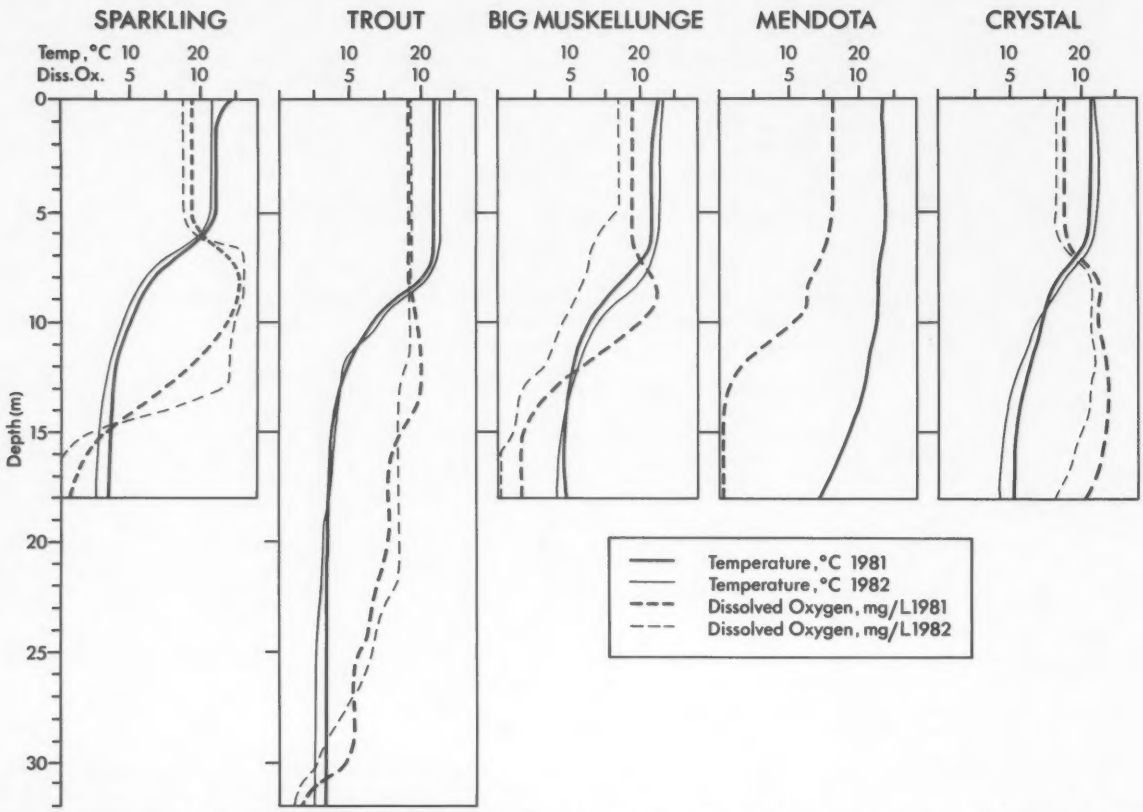

FIG. 2. Temperature and dissolved oxygen profiles in the five study lakes from 1981 and 1982. The profiles are from the fish sampling dates (see text). Lake Mendota was only investigated in 1981.

Muskellunge Lake (Table 4). The young-of-the-year (YOY) were in deeper water than older cisco in Sparkling Lake. In Trout Lake (1981), there was no significant difference in depth distributions of YOY and fish 140–189 mm long (93% of which were age 1+). Both groups, however, segregated from larger fish, which occurred in deeper water. In 1982, the 140- to 189-mm-long fish, now to 97% age 2+, were still segregated from older fish (Table 4).

Predicted and observed vertical distributions are presented in Table 5 and Fig. 3 and 4. Both predictions based on preferred temperatures and based on the temperature that results in best fit (BFT) between observations and predictions (maximum overlap of the two distributions) are presented. The BFT was calculated by systematically varying the value for the preferred temperature between 0 and 30°C. They range from 0 to 21°C for cisco and from 0 to 25°C for perch.

The observed distributions of all cisco in Big Muskellunge Lake and YOY cisco in Trout Lake were not significantly different from predictions based on the assumption that the final preferendum was 12–13°C. Thus, the vertical distributions of these populations can be predicted by final preferendum temperature and oxygen avoidance. However, the vertical distributions of cisco in Sparkling Lake and for 1- to 2-yr-old fish in Trout Lake were better described by assuming lower preferred temperatures (5–9°C). In 1981, older cisco in Trout Lake were distributed close to the bottom, and the temperature–oxygen model could not successfully predict their distribution using any temperature. Cisco in Lake Mendota had a BFT higher than the preferred temperature.

TABLE 3. Percent composition of catches in gill nets set between July 31 and August 24, 1981, and between July 27 and August 19, 1982 (see text for details on methods).

Lake	Year	% composition			Total caught
		Cisco	Perch	Other spp.	
Sparkling	1981	98	0	2	121
	1982	87	0	13	83
Big Muskellunge	1981	34	64	1	561
	1982	87	0	13	15
Trout	1981	86	13	1	173
	1982	98	2	0	283
Crystal	1981	0	90	10	94
	1982	0	98	2	44
Mendota	1981	34	61	5	406

The observed distribution of night-caught yellow perch in the epilimnion of Crystal Lake did not differ from the prediction based on their final temperature preferendum. The BFT's for other perch populations, with the exception of day-caught fish in Crystal Lake, were within 4° of the estimated final temperature preferendum. However, except for Crystal Lake, the model

TABLE 4. Comparison between depths occupied by young-of-the-year (YOY), 1+ and 2+, and older cisco in three Wisconsin lakes (Mann-Whitney *U*-test). The 25 and 75 percentiles are given in parentheses. All depths are in metres. In Sparkling and Big Muskellunge lakes there were not enough cisco older than 2+ caught to allow comparisons with that group of fish. For these lakes, the group 1+ and 2+ represent all older fish caught (predominantly those age groups). $^{**}P < 0.005$; $^{***}P < 0.001$; NS, not significant.

Lake	Year	Depth sampled	YOY median	*N*	1+ and 2+ median	*N*	Older median	*N*	Mann-Whitney *Z* score	*P*
Trout	1981	13–27	15 (14–18)	17	17 (14–19)	41			0.19	NS
		13–27	15 (14–18)	17			26 (22–27)	60	4.94	***
		0–27			16 (13–19)	47	26 (22–27)	63	7.63	***
Trout	1982	0–32			16 (14–18)	201	26 (17–29)	83	8.39	***
Sparkling	1981	0–18	13 (11–14)	73	12 (9–13)	39			2.76	**
Big Muskellunge	1981	0–18	10 (10–11)	119	10 (9–12)	67			0.46	NS

TABLE 5. Comparison of predicted and observed vertical distribution of cisco and yellow perch at the end of July and August, 1981 and 1982. Tabulated are the results of a Kolmogorov-Smirnov (K-S) test for predictions using the preferred temperature (12°C for cisco and 21°C for perch) and the temperature at which the model best fit observations. The range of temperatures for which the predictions are not significantly different from observations (range) and the measure of maximum overlap in percent (ovlp) between observed and predicted distributions are also given. Overlap is measured as

$$\left(\left(\sum_{b}^{c} |p_i - o_i|\right)\sqrt{2t}\right)\cdot 100\%,$$

where p_i = predicted number of fish at depth i, o_i = observed number of fish at depth i, b and c = the limits of the depth interval sampled, and t = total number of fish caught. $^{*}P < 0.05$; $^{**}P < 0.01$; NS, not significant.

		Preferred temperature			Best fit temperature					
Lake	Year[a]	K-S	*P*	ovlp	BFT	K-S	*P*	ovlp	Range	*N*
Cisco 1+ and older										
Sparkling	1981	0.464	**	51	8	0.139	NS	78	8–10	39
	1982	0.689	**	31	5	0.192	*	69	—	57
Big Muskellunge	1981	0.179	*	76	13	0.067	NS	80	13	68
Trout										
0–27 m	1981 (s)	0.614	**	37	9	0.153	NS	73	9–10	47
0–27 m	1981 (l)	0.854	**	13	0	0.231	**	70	—	63
0–30 m	1982 (s)	0.749	**	12	9	0.154	**	68	—	201
0–30 m	1982 (l)	0.861	**	14	6	0.242	**	68	—	83
Mendota	1981	0.388	**	61	21	0.260	**	69	—	137
Cisco YOY										
Sparkling	1981	0.695	**	31	6	0.056	NS	89	4–7	79
Big Muskellunge	1981	0.223	**	76	13	0.106	NS	76	13	123
Trout (13–27 m)	1981	0.053	NS	75	12	Same as preferred			8–15	17
Cisco, all ages										
Big Muskellunge	1982	0.265	NS	64	8	0.153	NS	77	2–12	13
Yellow perch										
Big Muskellunge	1981	0.684	**	32	18	0.273	**	59	—	324
Trout	1981	0.248	*	49	25	0.284	*	51	22	27
Crystal	1981 (N)	0.063	NS	89	21	Same as preferred			20–25	63
	1981 (D)	1.00	**	0	0	0.546	**	45	—	22
	1982	0.492	**	51	18	0.195	NS	72	18	43
Mendota	1981	0.173	**	75	23	0.239	**	76	—	250

[a]s, fish 140–189 mm long, predominantly 1+ in 1981 and 2+ in 1982; l, fish larger than 190 mm, predominantly 3+ and older; N, caught during the night; D, caught during the day.

based on BFT's did not successfully explain the observed distributions. The main difference between predictions and observations was the observed absence during the day of perch close to the surface. The depth to which 15% of the surface light penetrates appeared to correspond with the upper limits of the vertical distribution of perch during the day (Fig. 4). If daytime perch distributions in Trout and Big Muskellunge lakes and Lake Mendota are modelled assuming total avoidance of depth with light levels over 15% of surface light, the goodness of fit between predicted and observed distributions improves substantially in two of the lakes. For the final preferendum temperature, the maximum overlap increased from 32 to 75% in Big Mus-

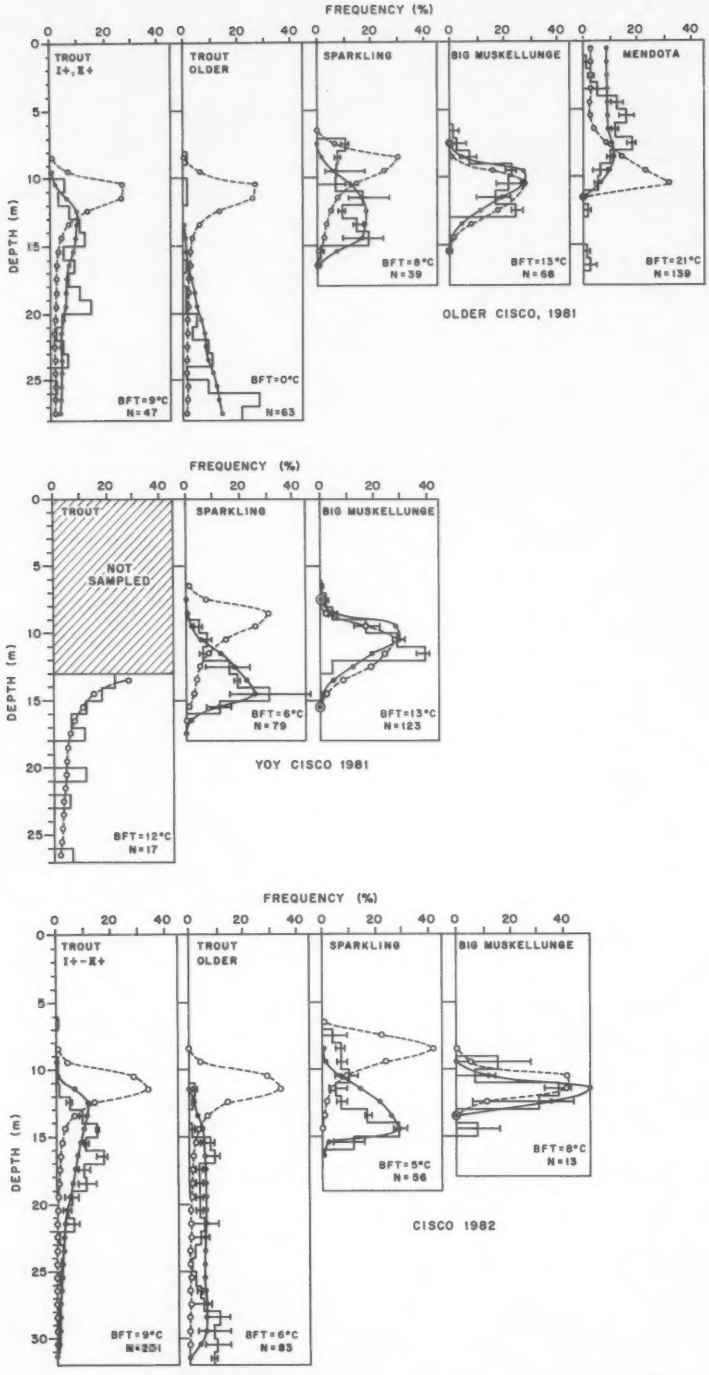

FIG. 3. Observed (histograms) and predicted vertical distributions of cisco: older fish in 1981, YOY fish in 1981, and all ages in 1982 in four Wisconsin lakes. The ranges for two 24-h sampling periods are included. Predictions based on both the preferred temperature (open symbols, 12°C) and on the temperature resulting in the best fit between predictions and observations (BFT) (solid symbols) are presented.

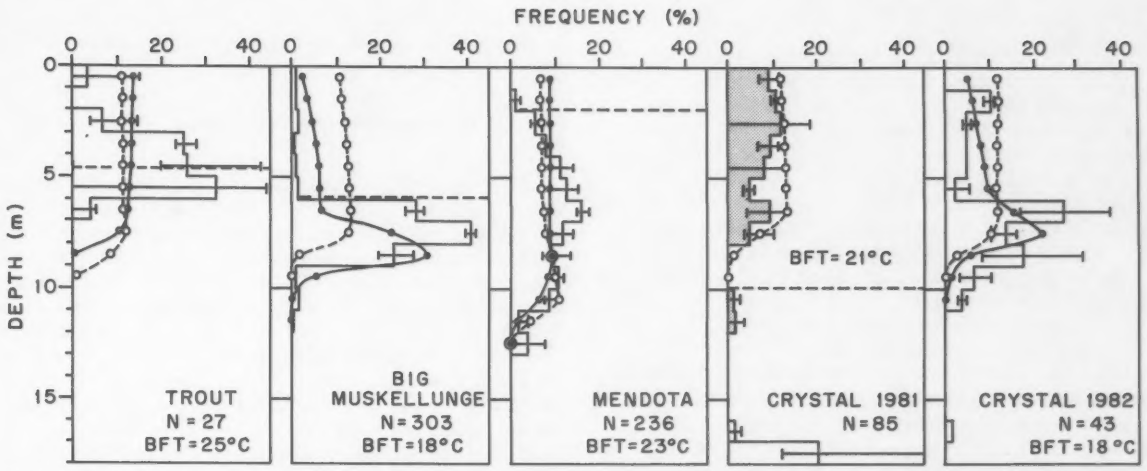

FIG. 4. Observed and predicted vertical distributions of yellow perch in five Wisconsin lakes. The ranges for two 24-h sampling periods are included; day and night are not separated. Predictions based on both the preferred temperature (open symbols, 21°C) and on the temperature resulting in the best fit between predictions and observations (BFT) (solid symbols) are presented. Fish caught at night in 1981 (only Crystal Lake) are marked with shaded bars. The perch in the other lakes were caught during the day. The broken line in the graphs for 1981 represents the depth for 15% of surface light.

kellunge Lake and from 75 to 86% in Lake Mendota. The BFT is then 19°C (86% overlap) in Big Muskellunge Lake and the same as the final preferendum in Lake Mendota. In Trout Lake the goodness of fit did not improve. A more detailed analysis with these data was not profitable, since surface light levels were not measured during the sampling dates.

Discussion

Our approach offers a new and systematic way to analyze the vertical distribution of fishes in gradients of temperature and oxygen. Knowledge of relative preference of fish to a range of temperatures and oxygen concentrations is incorporated, rather than the assumption of a single preferred temperature and a single avoidance oxygen concentration. The model represents our best estimate of fish behavior in response to temperature and oxygen. It can be regarded as a null hypothesis stating that only temperature and oxygen governs fish distribution. These variables were obvious choices for inclusion in a first model, since it has long been known that temperature and oxygen are important for fish distribution (e.g. Juday and Wagner 1980; Fry 1937; Frey 1955). Other environmental factors can be incorporated if comparable knowledge exists for the response of fish to them. Successively more complete models for fish distribution can thus be constructed, but their complexity increases rapidly with the number of variables included.

In general (Fig. 5; Table 5), the agreement between predictions and observations was higher for best fit temperature than preferred temperature, and better for cisco than for yellow perch. For best fit temperature for cisco, the percent overlap between observed and predicted distributions was greater than 68% in 12 out of 12 cases (Table 5). Poorest agreement was for yellow perch preferred temperature which ranged from no overlap between observed and predicted to 89% overlap. Some of the observed distributions (Big Muskellunge 1981 and 1982 for cisco, Trout 1981 for YOY cisco, and Crystal 1981 for perch caught at night) were not significantly different from model

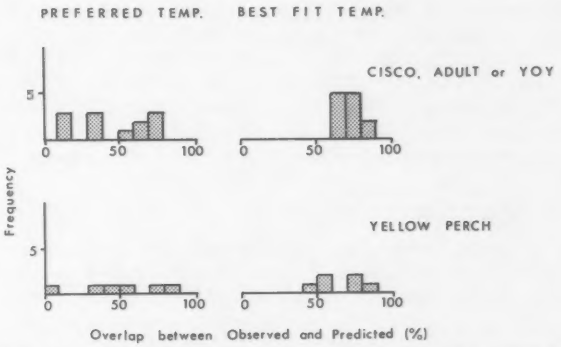

FIG. 5. Distribution of overlap values for cisco and yellow perch. Both values for preferred temperature (12°C for cisco, 21°C for perch) and for best fit temperature are presented. For more details see text and Table 5.

predictions based on a temperature within 1° of our estimated preferred temperature (Table 5). In other lakes, the oxygen–temperature model was rejected. We use the cases where the agreement between prediction and observation was poor to help identify the possible importance of other factors; hypotheses more complex than our temperature–oxygen model are required to understand and predict the vertical distribution of perch and cisco. Hypotheses that might be relevant are as follows: (1) the final preferendum is not species-specific but varies among populations in different lakes and among age groups; (2) the preferred temperature decreases at low oxygen levels; (3) the fish choose to occupy a temperature lower than their final preferendum to optimize growth rates in lakes with limited food; (4) factors other than temperature and oxygen are important for determining the vertical distribution of the two species.

Comparisons of goodness of fit and direction of deviations from predictions can give indications as to which hypotheses are most tenable. These are discussed below.

1. The Final Preferendum as a Species-Specific Response

For cisco, the differences in best fit temperatures among lakes and age groups could be the result of differences in final preferendum among populations. Cisco is a morphologically variable species; McPhail and Lindsey (1970) considered it a species complex, and several populations studied in Wisconsin were considered to be different subspecies by Koelz (1931). However, there is little evidence for any geographic variation in preferred temperature (Beitinger and Fitzpatrick 1979). Also, the distributions observed in Sparkling and Trout lakes require a preferred temperature of between 5 and 9°C in the model; such low preferences are unlikely, since they are lower than observed for any other salmonid (see Coutant 1977).

The final preferendum can also decrease with age as observed for the confamilial rainbow trout and for yellow perch (McCauley and Huggins 1979). The prediction would be that older fish occur at deeper depths than younger fish. The segregation of 1- to 2-yr-olds in shallower water than older fish in Trout Lake correspond with this prediction. However, no such separation of cisco age groups was found in Big Muskellunge or Sparkling lakes; and in Sparkling Lake, the YOY were caught significantly deeper than older cisco.

The above inconsistencies cause us to doubt that genetically fixed differences in temperature preferences — among different populations or different age groups — explain the variation in temperature occupation among and within lakes.

For perch, overlap between predicted and observed distributions was low for any temperature used in the model. A preferred temperature lower than 20°C is not likely, since all studies on temperature preference of perch have found the final preferendum to be at least 20°C. Thus, other factors must be important.

2. Effect of Low Oxygen Levels

Bryan et al. (1984) recently reported a substantial decrease in preferred temperature of the plains minnow (*Hybognathus placitus*) at low oxygen levels (from 30°C at 4.0 mg/L to 17°C at 2 mg/L). The preferred temperature corresponded to the highest temperature at which the fish could maintain respiratory independence. However, this effect cannot explain why cisco occupy colder water than expected in the northern lakes. Water with sufficient oxygen and final preferendum temperature was available to the fish (Fig. 2). The extreme situation in Lake Mendota resulted in the cisco occupying warmer temperatures than predicted by our model.

3. Bioenergetic Considerations

The relatively good fit for cisco predictions based on lower temperatures than the final preferendum indicates that they might be choosing such temperatures even when the final preferendum is available to them. This could result in better growth when food is limiting because it would reduce metabolic cost (Brett 1979; Crowder and Magnuson 1983). Because growth of cisco is inversely related to density in the northern lakes (Hile 1936; Rudstam 1984), food may indeed be limiting for these populations. Thus, this explanation may have some validity.

Occupation of colder water only during nonfeeding periods to reduce energetic costs (Brett 1971) does not appear to occur; no diel vertical migration was detected in our study lakes. Also, because cisco appear to feed both day and night there may not even be a "nonfeeding" period in which it would be beneficial to reduce metabolic costs. Volume of stomach contents from fish caught in Trout Lake during different periods of the day did not differ (L. G. Rudstam, pers. obs.).

4. Vertical Distribution and Other Factors

Light

Light is probably an important additional factor influencing vertical distributions, at least for perch caught during the day. For these perch, deviations from predicted distributions based on temperature and oxygen resulted from the fish not being caught close to the surface. The deepest catches of perch during the day were registered in the lake with the clearest water (Crystal) and the shallowest catches in the lake with the most turbid water (Mendota). Perch caught at night in Crystal Lake in 1981, when light would be less important, did not avoid the surface waters, and their distribution fit the temperature–oxygen model quite well. We do not believe that this was an artifact of diel differences in net visibility because sonar charts showed similar vertical distributions to the net catches (Rudstam 1983). The goodness of fit between predictions and observations improved substantially in Big Muskellunge Lake and Lake Mendota when predictions were restricted to water below the depth of 15% surface light. In the laboratory, brook trout, *Salvelinus fontinalis* (Sullivan and Fisher 1954), and bluegills, *Lepomis macrochirus* (Stuntz 1975), occupied nonpreferred temperatures to avoid high light intensities. Light could also be a factor keeping cisco in deeper water than predicted as suggested by S. F. Hamrin (Institute of Limnology, University of Lund, Sweden, pers. comm.) for vendace (*Coregonus albula*).

Inter- and intra-specific segregation

Differences in preferred temperature among fish species may result in habitat segregation (MacLean and Magnuson 1977; Brandt et al. 1981) with or without active avoidance of other species. We found no evidence of vertical segregation in the water column between cisco and perch beyond that expected from their different temperature preferenda. Typically, perch were above cisco as expected. Cisco were actually distributed at lower temperatures when perch were rare (Trout and Sparkling) than when perch were common (Big Muskellunge). In Lake Mendota, the two species occupied the same depths. This does not preclude interactive segregation on other niche axes. Perch and cisco are usually caught in the pelagic habitat at different times of the day, perch during the day and cisco at night (Engel and Magnuson 1976; Rudstam 1983). At night, perch were only caught in midwater in Crystal Lake, which contained no cisco.

Differences in vertical distributions among age classes of cisco in two of the lakes indicate that intraspecific segregation may be important. Other investigators have found young coregonids in warmer, shallower water than the older age groups (Fry 1937; Valtonen 1970). Sparkling Lake is an interesting exception in that younger fish appear to be at the same depth as older cisco or somewhat deeper. The YOY cisco may be avoiding rainbow smelt, *Osmerus mordax*, which occupy temperatures around 16°C (pers. obs.), or potential cool-water predators such as walleye, *Stizostedion vitreum vitreum*, and muskellunge, *Esox masquinongy*.

Food distribution

We did not investigate the vertical distribution of food particles in this study. Prey availability probably accounts for some of the observed patterns in fish distribution. For example,

chironomids are abundant in the aquatic moss growing at the bottom of Crystal Lake to a depth of 21 m and are an important part of perch diet in that lake. This can account for the day distribution of perch close to the bottom of Crystal Lake in 1981. Prey availability may also be a factor in the occurrence of older cisco close to the bottom of Trout Lake.

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The Distribution and Abundance of Seals in the Canadian High Arctic, 1980–82

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Surveys of hauled-out ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) were flown in 1980 and 1981 over Jones Sound, the Sverdrup Basin, the channels between the Parry Islands, the Parry Channel, Prince of Wales Strait, and northern Amundsen Gulf. Part of the survey was flown again in 1982. Ringed seals were most numerous in Barrow Strait and Wellington Channel, their density decreasing westward and northward. Their preferred habitat was annual ice, fast or cracking, of high cover; they avoided deep water. Bearded seals were seen in low numbers in early-opening areas, preferring floe or rotten ice of moderate or low cover over shallow water.

En 1980 et 1981, on a effectué des relevés aériens du phoque annelé (*Phoca hispida*) et du phoque à barbe (*Erignathus barbatus*) présents sur les glaces du détroit de Jones, du bassin Sverdrup, des chenaux entre les îles Parry, du chenal Parry, du détroit Prince of Wales et de la partie nord du golfe Amundsen. Une partie du relevé a été répété en 1982. Le phoque annelé était plus abondant dans le détroit de Barrow et le chenal Wellington; sa densité diminuait vers l'ouest et le nord. Pour son habitat, il préférait la glace de l'année, fixée ou fissurée, de grande superficie et évitait les eaux profondes. Quant au phoque à barbe, un faible nombre a été observé dans les régions de débâcle hâtive; il préférait la glace pourrie ou les floes de petites ou moyennes dimensions en eau peu profonde.

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In the early and mid-1970's, several large-scale resource extraction projects were proposed for the high Arctic, all affecting marine areas. The Arctic Pilot Project proposed to ship natural gas from Melville Island, and Dome Petroleum to ship oil from the Beaufort Sea, to eastern markets through the Northwest Passage. The Ministry of Transport (1981) estimated 897 total marine passages a year in the Arctic by 1995; but the Canadian Arctic Resources Committee (CARC) (1980) estimated 1000 a year in the Northwest Passage alone by 2000. Exploratory drilling for hydrocarbons is underway or proposed in the Sverdrup Basin, Lancaster Sound, and Viscount Melville Sound. The Arctic Islands Pipeline Project proposed crossing several interisland channels to pipe natural gas to southern markets, and other suggestions have been made for shipping routes, pipelines, and mines in the high Arctic (CARC 1978; Dirschl 1980; Keith et al. 1981).

In response to these proposals, several short-term, site-specific environmental assessment studies of various marine mammals have been carried out (e.g. Finley 1976, 1979; Finley and Johnston 1977; Davis et al. 1978; Smith et al. 1978; Smith and Hammill 1980).

The study reported here was designed, on a larger scale, to evaluate the distribution and abundance of seals in the high Arctic in the major interisland channels where activities have been proposed — northern Amundsen Gulf, Prince of Wales Strait, Viscount Melville Sound, Barrow Strait, and the southern Sverdrup Basin — and the relative importance of each area to the different species, so that the most important areas could be identified for special consideration.

Three species of pinniped are resident in the Canadian high Arctic: the ringed seal (*Phoca hispida*), the bearded seal (*Erignathus barbatus*), and the walrus (*Odobenus rosmarus*). Although the natural history and general biology of these species have been studied in other areas (e.g. Chapskii 1938, 1940; McLaren 1958a, 1958b; Mansfield 1958; Loughrey 1959;

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Burns 1967; Smith 1973a, 1973b; Smith and Stirling 1975, 1978; Smith and Hammill 1981), there was, until about 10 yr ago, little information, and that mostly anecdotal, on the distribution and abundance of these species in the Arctic archipelago (e.g. Vibe 1950; Mansfield 1967; Bissett 1968). Even basic information on the harvests of marine mammals by Inuk hunters has not been collected (Davis et al. 1980).

The phocids, particularly the ringed seal, were selected as target species for several reasons: they are pinnipeds with general and opportunistic diets, and so should act as indicator species for general levels of biological production; they are of economic and subsistence value, both directly and by supporting the polar bear (*Ursus maritimus*); and they can be readily counted from the air when they haul out to moult on the ice in early summer, allowing comparative information on large areas to be gathered accurately and relatively cheaply.

Although the distribution of walrus was of interest, both per se and relative to that of the seals, wide-area surveys are not well suited to determining it. The species is not widely distributed, although locally abundant, is very highly clumped, and, owing to its habit of hauling out on land, is apt to be missed by ice-directed aerial survey.

The survey was a medium-altitude, systematic, strip transect, aerial sample survey. Ringed and bearded seals hauled out were recorded only when they were within the transect strip; we also recorded incidental sightings of walrus, polar bear, narwhal (*Monodon monoceros*), and beluga (*Delphinapterus leucas*).

Methods

Study Area

The study area comprised the Parry Channel from 117°20′W to 90°40′W, the Sverdrup Basin north to 78°10′N between 110°W and 88°W, Jones Sound east to 86°W, Prince of Wales Strait, and Amundsen Gulf west to 120°40′W and south to 71°N (Fig. 1).

We expected that the study area would not be homogeneous and that seal densities would vary from area to area. Consequently, we divided it into 10 strata, based on natural separations of water bodies, known currents, and patterns of breakup. The rectilinear stratum boundaries of Fig. 1 were drawn to approximate the perceived natural boundaries while facilitating stratified analysis of the data.

Currents flow through the study area generally south and southeast, from the Arctic Ocean to Davis Strait (Fig. 1). The water coming in from the Arctic Ocean is cold, has had little nutrient mixing, and has been screened from sunlight by ice cover, reducing the amount of photosynthesis that could occur. Strong currents in the Byam Martin Channel, Penny Strait, and Hell Gate extend open water seasons, allowing sunlight to stimulate photosynthesis, and may cause nutrient mixing. Therefore, the area north of these channels was separated from the area to the south. The northern area was divided into three: Norwegian Bay (stratum 2) is shallow, and lies upstream of the Hell Gate polynya and currents in Belcher Channel; the Prince Philip Basin (stratum 3) is somewhat deeper, and feeds the Penny Strait – Queens Channel polynya; and stratum 4, deeper yet, feeds the currents through the Byam and Austin channels (Fig. 1). Among these three strata, the amount of old ice decreases, and the extent of open water in summer increases, from west to east. In some years, parts of strata 3 and 4 hardly break up at all.

Jones Sound (stratum 1) is naturally separated from the others by being downstream of the strong currents and reliable polynyas in Hell Gate, Cardigan Strait, and Fram Sound. It contains some very deep (to 600 m) water. It breaks up almost completely every year, but may contain some multiyear ice that drifted in from further north.

Strata 5 and 7 consist of the channels between the Parry Islands. Stratum 5 is downstream of currents from stratum 3, which usually has some open water in summer at the northern end of Penny Strait; it contains several recurring polynyas and is usually ice-free in summer. Stratum 7 is downstream of the multiyear-ice areas of stratum 4 and tends to contain floes of old ice that drift south. The ice edge across Byam Martin Channel is keystoned by Byam Martin Island, so that breakout of the channel is usually late or incomplete. The stratum is shallow, and the south-setting current in Byam Martin Channel creates small polynyas early in summer around the points of the islands west of Bathurst Island.

Stratum 6 (Barrow Strait) is downstream of stratum 5 and also receives currents from stratum 8. It is known to be a biologically active area with summering narwhals and white whales and feeding seabirds from the large colonies in Lancaster Sound. This area is covered with annual ice only and is one of the first to break up: the ice edge usually reaches Griffith Island by early or mid-July.

Stratum 8 is deeper than stratum 6 and receives water from Byam Martin Channel (stratum 7) and Viscount Melville Sound (stratum 9). It breaks up later than stratum 6 and is usually free of ice each year, although its western end may have some multiyear floes which have come through the Byam Martin Channel.

Stratum 9 is the deepest of those along the Parry Channel and receives water only from the west. It generally breaks up late and incompletely and contains much multiyear ice. It appears to be less biologically productive with few seabirds and marine mammals, although polar bears are quite abundant northeast of Victoria Island (Stirling et al. 1978).

Prince of Wales Strait and northern Amundsen Gulf (stratum 10) are relatively shallow (50–150+ m) and covered with annual ice; breakup is complete in most years. Currents are from the north, but the extent to which they mix in the stratum with water from southern Amundsen Gulf is not clear. Earlier studies indicated that Amundsen Gulf had high ringed seal productivity (Smith and Stirling 1975).

Survey Design

The survey was designed as a systematic, strip transect, sample survey (Fig. 1). Transects were oriented north–south over the whole study area so that great-circle navigation would be easier, were spaced every 40′ of longitude, and were 1/2 mile (804.5 m) in net width.

Because of the convergence of meridians, the sampling rate varied from north to south, highest (5.2% at 78°) in the northern areas and lower (3.9% at 74°; 3.3% at 71°) further south.

Survey Flying

The survey was flown in a Cessna 337 "Skymaster" at its normal cruising speed of about 130 knots, and at a target altitude of 500 ft (152.4 m), with 300 ft (91.4 m) as an alternative when visibility was poor in fog or low cloud. The transect — 1/4 mile (402.3 m) wide on each side of the aircraft, net of the blind strip underneath — was divided into inner and outer 1/8-mile strips.

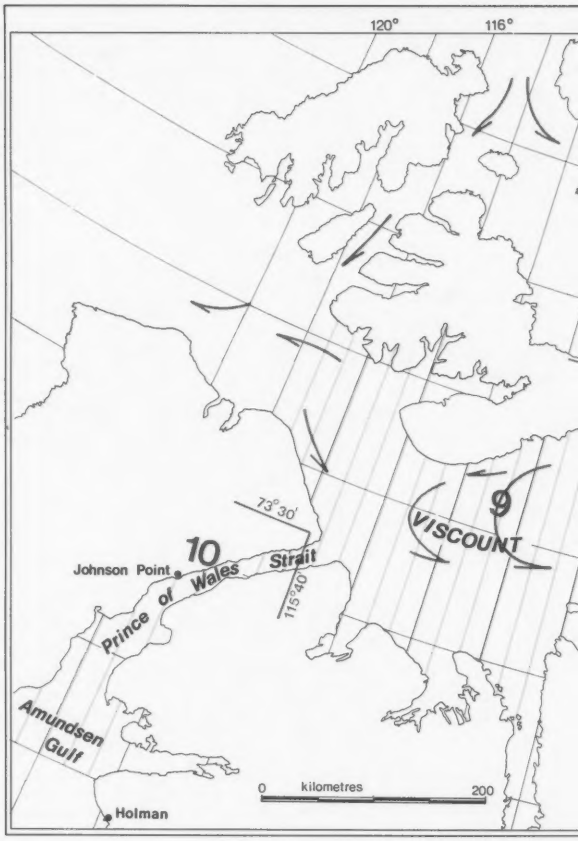
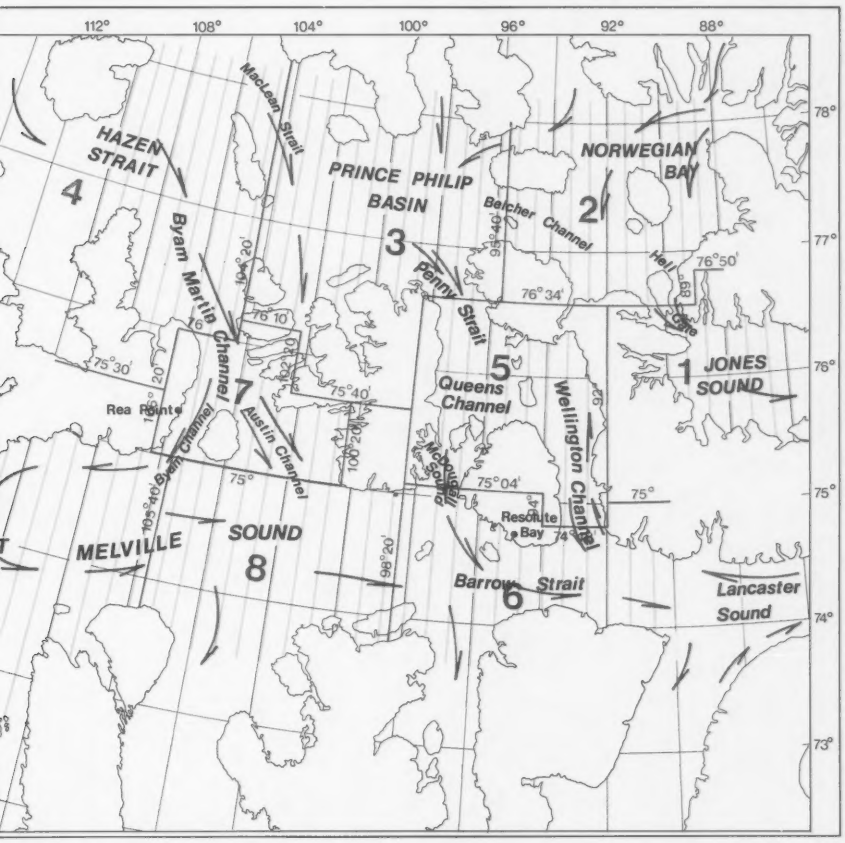


FIG. 1. Study area, transect lines, and stratum boundaries f



ndaries for the high Arctic seal survey, with principal currents (after Smiley and Milne 1979).

The strip boundaries were determined by the observers by aligning a mark on the window with marks on the wing struts. The struts were marked as follows: with the aircraft parked on level ground, each observer got in and marked his window at a convenient height for viewing; the height of the mark from the ground was then measured, and the strip width was reduced in proportion from 1/8 mile at 500 ft; marks were made on the ground at the reduced distances from the inmost visible point, and the other observer aligned the strut mark with the marks on the ground and the window. This method is quick and simple, but probably only usable with aircraft like the Cessna 337 which have tricycle gear. The same observers sat in the same places in 1980 and 1981.

All data were recorded by 2-min intervals. When the aircraft crossed the shoreline at the start of a transect, a stopwatch and a quartz-crystal 2-min beeper were started. The beeper prompted the observers to start a new line on the data recording form; the stopwatch gave total duration of the transect, and could be used by either observer to time flight over intervening islands or headlands and get an effective duration for each affected interval. Navigation was by Omega-GNS 500 Global Navigation System. The starts and ends of transects on shorelines were checked on 1 : 500 000 topographic maps, and the true starting and ending latitudes were recorded.

All seals hauled out on ice were identified to species and recorded as being in the inner or outer strip. Seals in water were not counted, because they were subject to quite different visibility biases, and could not easily be identified.

In 1981, seal breathing-holes were also counted, but took second place to the accurate recording of seals. As this was partly experimental, we did not agree beforehand on standard rules for deciding what was or was not a breathing hole, nor for when seal holes could or could not be inferred, under snowdrifts or pressure ridges, from drainage patterns, bear tracks, or other clues. Instead, each observer operated his own set of criteria.

Three ice variables were recorded: cover, age, and condition (Table 1). Cover, in eighths, was recorded by each observer; age and condition were recorded only by one, and the other recorded the cloud cover and a wind speed estimate given by the pilot (Table 1). Data were recorded on a keypunchable field sheet.

A data file of water depths was built by taking the latitudes of boundaries between depth classes off standard hydrographic charts (Kingsley and Stirling 1982).

In 1980, the survey was flown between 21 June and 8 July, and in 1981 between 21 June and 10 July.

Stratum 6 had much open water when the survey was flown in 1981, so it was flown again in 1982. The opportunity was also taken to fly stratum 5, to confirm the high densities previously found there, and stratum 1, to confirm the low densities. These strata were flown between 1 and 3 July 1982.

Amundsen Gulf was also surveyed in 1982. The area covered was not exactly the same as stratum 10, extending south to 70°30′N and west to 123°W, but north only to 72°N. However, results from that survey are included here for comparison with those of 1980 and 1981; it was flown between 21 and 24 June 1982.

TABLE 1. Data recorded.

Variable	Value(s)	Description
Ice cover	0–8	Ice cover in eighths. In particular, 8/8 ice is not necessarily unbroken ice, but 0/8 is open water with no ice
Ice age[a]	1	Annual ice: formed the previous winter
	2	2-yr ice: formed 1.5 yr ago
	3	Ice older than 1 yr but not certainly identifiable as 2 yr or multiyear
	4	Ice certainly older than 2 yr
Ice condition[a]	Fast	Solid ice, no breakup
	Cracking	Ice starting to break up. Leads or cracks far to very far apart (5–20 km); cracks in a matrix of ice
	Large floe	Floes more than 0.5 km in size, floes in a matrix of water
	Small floe	Floes less than 0.5 km in size
	Rotten	Thin, dark-grey or black ice; numerous thaw holes
Sky condition	Clear	No cloud shadow on or near the transect line
	Scattered	Up to 50% cloud shadow on or near the transect
	Broken	50–90% cloud shadow on or near transect
	Overcast	No sunshine on or near transect
Wind speed	0	No wind
	1	1–5 knots
	2	6–10 knots
	3	11–15 knots
	4	16–20 knots
Duration	0–120	Time in seconds in 2-min interval which was spent over ice or water. In 1980, recorded to nearest 10 s. Recorded separately by left and right observers
Fog	Light fog	Visibility to 1/4 mile; often possible to fly at 500 ft; good counts on at least inner 1/8-mile strip
	Fog	Necessary to fly at 300 ft or to abandon transect; no good counts

[a]Where "ice type" is referred to in the text, it includes both age and condition.

Data Analysis

The analysis of data will be described in four phases: completion, habitat regression, density estimates, and comparison of observers. In completing the data, we added to the counts of seals and holes for each 2-min interval information on the area surveyed, the sun time, the transect spacing, and the water depth. The fundamental assumption was that ground speed had been constant over the transect. The length of each transect was calculated from its starting and ending latitudes and divided by the elapsed time to give the speed. The centres of the 2-min intervals were interpolated along the transect and their effective areas found from the speed and the effective durations. Each interval, then, had the following: latitude and longitude (of its centre), local time, counts of seals and holes, ice records, weather records, and area. Now more attributes could be deduced: local time was converted to sun time by assuming a sun time of 12:00 at 0° longitude at 12:00 GMT and assuming the earth to rotate uniformly at 15°/h; transect spacing was calculated from the latitude; stratum number was calculated by comparing the coordinates with the stratum boundaries of Fig. 1; and water depth was looked up in the specially built data file (Kingsley and Stirling 1982). In all calculations, the earth was

TABLE 2. Variables created for regressions from habitat and weather and time records.

Variable family	Variable names	Formation
Ice age	Annual, older	"Annual" set[a] only if ice age = 1; "older" set only if age >1
Ice condition	As variable value in Table 1	Binary variable set only if ice condition equal to variable name
Cover	Any, 1plus–7plus, 8	*i*th binary variable set if cover equal to or greater than *i*/8[b]
Sky condition	Scatplus, Brokplus, Overcast	Scatplus set if cloud over 0; Brokplus set if cloud cover >50%; Overcast set if cloud cover = 100%[b]
Depth	dg1–dg10	dg1 set if depth class >1; up to dg10 set if depth class >10[b]
Stratum	strat1–strat10	*i*th binary variable set if stratum equals *i*
Wind	wind1p–wind4p	*i*th binary variable set if wind speed ≥ class *i*[b]
Fog	anyfog, thickfog	anyfog set if fog or light fog; thick fog set if fog[b]
Sun time	stgt9–stgt17	stgtHH set if sun time > HH:00[b]
	st13	A continuous variable equal to sun time (in hours) minus 13. It tested for a general increase (or decrease) in density through the day
	st13sq	A continuous variable, the square of the previous one. It tested for a midday peak (or trough) in density

[a]A binary variable is said to have been "set" if its value is 1; its only alternative value is 0, and it is then said to have been "cleared."

[b]These families of binary variables were all cumulative: if a member of the family was set, all lower members were also set (for example, in ice cover, if "3plus" was set, "any," "1plus," and "2plus" were also set) (cf. Draper and Smith 1981, p. 246, ex. 2); the other families were exclusive, so that one and only one would be set in each family.

assumed spherical, 1′ of latitude equal to 1852 m, and 1 statute mile equal to 1609 m.

When we had not flown parts of transects because of fog or because they were open water, we added records to the data for them. The known length of unflown transect was divided into segments that would each have taken about 2 min to fly, and a data line was made up for each such segment. The ice types for segments unflown because of fog were inferred from neighbouring transects and checked on weekly composite ice charts (Ice Forecasting Central, Environment Canada, Atmospheric Environment Service, Downsview, Ont.). These dummy records were not used for estimation of stratum mean density, only for estimation of stratum area, ice type composition, and stratum population.

The habitat preferences of ringed seals were investigated using stepwise regression. The density was regressed on binary variables created from the depth, ice, weather, and time records (Table 2). The sampling unit was the 2-min interval; very small segments (less than 25%) arising from short effective durations were dropped. The regressions were unweighted either for variation in sampling density or for variation in the size of the sampling units due to speed variation between transects.

Calculations of stratum and overall mean densities used the transect longitude as the sampling unit. The count and area for each interval were extended by the transect spacing at that point, and then summed over the transect:

$$(1)\quad Y_i = \sum_{j=1}^{J_i} W_{ij} t_{ij}$$

$$(2)\quad X_i = \sum_{j=1}^{J_i} W_{ij} A_{ij}$$

where Y_i = extrapolated total seals on ith transect longitude, W_{ij} = transect spacing for jth interval on ith transect (in transect-widths), t_{ij} = seals counted in jth interval, J_i = number of intervals on ith transect, X_i = extrapolated total area of ith transect longitude, and A_{ij} = area of jth interval.

The estimated stratum mean density was given by the standard ratio estimate (Cochran 1977)

$$(3)\quad \hat{R} = \sum_{i=1}^{I} Y_i \Big/ \sum_{1}^{I} X_i$$

where I = number of transects in the stratum.

Two estimates of standard error were calculated. The first was that appropriate to random sampling:

$$(4)\quad S_1^2 = I \sum_{1}^{I} d_i^2 / \{(I-1)\cdot(\Sigma X_i)^2\}$$

where (Cochran 1977)

$$d_i = Y_i - \hat{R} X_i.$$

However, the sampling in this survey was not random, but systematic. Under certain common conditions of positive correlation between neighbouring units, systematic sampling is more precise than random (Cochran 1977, p. 220–223), but the within-sample variance S_1^2 then overestimates the sampling error variance (Cochran 1977, p. 208); i.e. it underestimates the precision. Under such conditions, a variance estimate based on first-order serial differences may be less biased (Kingsley and Smith 1981) but may still underestimate the precision of the survey (Cochran 1977, p. 225).

A variance estimate based on the serial differences of the d_i is obtained by modifying eq. (3) according to Cochran (1977, p. 225, eq. 8.44) to give (Kingsley and Smith 1981)

$$(5)\quad S_2^2 = \left\{ I \sum_{1}^{I-1} (d_i - d_{i+1})^2 \right\} \Big/ \left\{ 2\cdot(I-1)\cdot(\Sigma X_i)^2 \right\}.$$

(Note that the finite population correction $1 - f = (N - n)/N$ has been ignored owing to the small sampling fraction.)

If seals were randomly and independently distributed, the expected values of S_1^2 and S_2^2 would be equal, and the error coefficient of variation would be

$$1 \Big/ \sqrt{\sum_i \sum_j t_{ij}}.$$

As measures of the nonindependence of seal distribution, we calculated clump factors C_1 and C_2 from

$$(6)\quad C_k = S_k^2 \Sigma\Sigma t_{ij} / R^2, \quad k = 1, 2.$$

Stratum mean densities of ringed seals were calculated for levels of ice cover (6/8+) shown by the habitat regressions to be preferred habitat. Few seals were seen on ice of lower cover, and the calculation of density on defined habitat gave meaningful comparisons between strata, unaffected by the stratum mean ice cover.

We compared left with right observers and inner with outer strips by calculating, from data selected for high ice cover and clear visibility, unstratified mean densities and standard errors for left observer, right observer, inner strips, outer strips, and total. A components of variance model was invoked to provide a sensitive test of difference. Each transect may be regarded as having a long-term mean density of seals, varying from transect to transect. Because the survey only covered a sample of transects, there was a component of error, σ_a^2, which represents the incorrectness of inferences about the areas that were not covered. Also, the actual density obtained for any transect would be expected to differ from its long-term mean, introducing the second component of error, σ_b^2. The second component was halved when the two observers were averaged, but the first was unaffected. Therefore:

$$E(V_w) = \sigma_a^2 + \sigma_b^2/2$$

$$E(V_s) = \sigma_a^2 + \sigma_b^2.$$

V_w was estimated by S_2^2 for the whole transect and V_s by the mean of the S_2 values for left, right, inner, and outer strips. Then, the appropriate error term for tests between observers or between strips was

$$\sigma_b^2 = 2(V_s - V_w).$$

Densities were compared only on the best data: no fog or rain, 6/8+ cover recorded by both observers, and durations of 120 s for both observers.

Results and Discussion

Ice Conditions on Strata

The distribution of annual and multiyear ice in the high Arctic is self-perpetuating; multiyear ice is thicker than annual ice, and slower to melt and break up, so it tends to stay, and get older, while the annual ice tends to melt completely every year; 2-yr-old ice is rare (Lindsay 1975, 1977). There were higher proportions of annual ice in all strata in 1981 than in 1980 (Fig. 2; Table 3). The ice cover at survey time was about the same in the two years in all strata except 6 and 10, where it was lower in 1981 (Table 4; Fig. 3), but much of the annual fast ice in strata 5, 6, and 8 looked thinner (greyer) in 1981 than in 1980.

In 1981, breakup was somewhat further advanced at survey time. Strata 4, 7, 8, and 9 were 100% fast ice in both years, but the others all had lower proportions of fast or cracking ice in 1981, and more floe or rotten ice (Table 3; Fig. 3). The 1980 situation in Barrow Strait was close to the "early spring" of Bradstreet and Finley (1977, fig. 0-1); in 1981 it was like their "late spring."

In 1982, stratum 10 was still 100% fast ice when the survey was flown; the fast-ice edge ran nearly straight from Nelson Head to Cape Parry. Barrow Strait (stratum 6), which the 1981–82 winter had not frozen fast until mid-February, was still mostly fast ice in early July 1982 (Fig. 3). Ice cover and the percentage of fast ice were also higher in strata 1 and 5 than they had been in 1980 or 1981.

Between years, the ranking of strata by percentage annual ice agreed very closely and the ranking by percentage fast ice agreed exactly.

Areas that break up completely break up early, leading to an association in our data between the fast condition and multiyear age, and between cracking, rotten, and large-floe conditions and annual age. Small-floe ice was rare at survey time, but was weakly associated with multiyear age because of the differential rate of melting: by the time the ice is down to the small-floe stage, older ice is forming a larger proportion of what is left.

Survey Quality

Seals hauled out on dry, clean, white ice were very visible, and far from camouflaged; in addition, drainage patterns on the ice led the observer's eye to seal holes near which seals might be seen. We found the best viewing conditions to be a thin overcast with diffuse light, no glare, and no strong shadows — seals then stood out very black against their background.

The ground speed realized on transect was variable, depending on the wind, and averaged 130 knots in 1980 and 131 knots in 1981. At a density of 1.5 seals/km^2 — high for this survey — this gave an observer an average of 25 s to see and count each seal; the average counting rate over the whole survey for each observer was 0.51 seal/min. Seals in the middle of the transect strip were in sight for about 25 s, those nearer the aircraft a shorter time, and those further out for much longer. In general, we had no trouble seeing and counting seals or keeping up with the count, but were occasionally kept busy in small areas of high density.

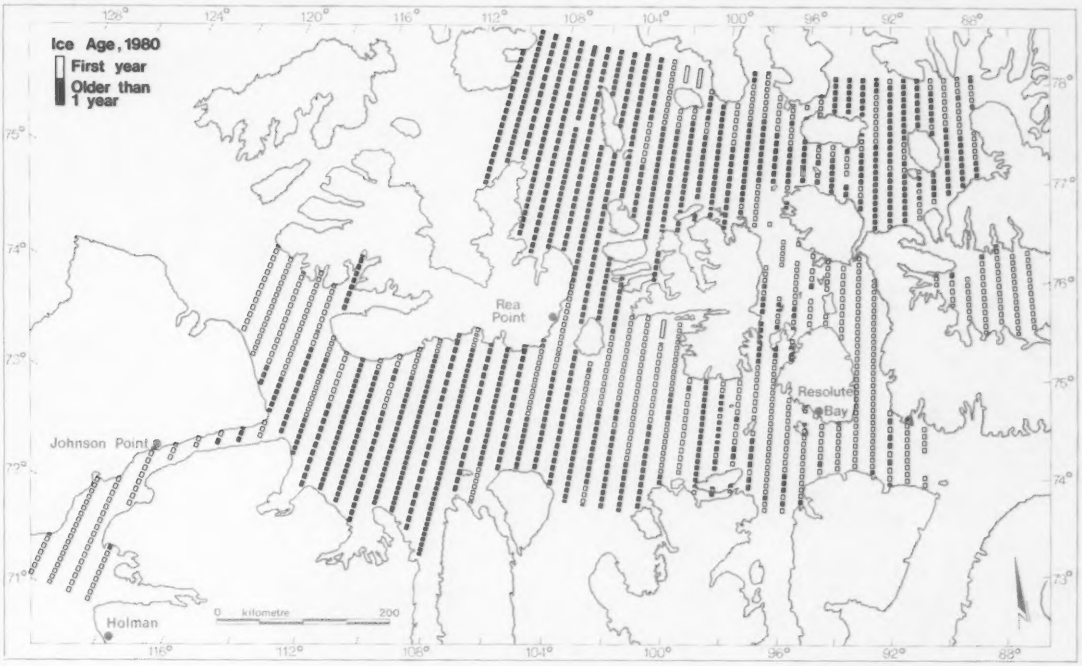
In 1980 and 1981 we were unable to fly some transects because of fog and others because of logistical problems, and omitted some because they were open water. The areas so lost were small: 1.07% of the survey in 1980; 2.12% in 1981, mostly open water in Amundsen Gulf.

Errors to be considered in population estimation by sample survey fall into two classes: sampling and nonsampling errors.

Sampling error is the error incurred by assuming that the sample has the same mean density as the whole study area. It is random and variable from stratum to stratum. It can be reduced by taking large samples and often by systematic sampling, and can be estimated by statistical methods. Our sampling fraction varied from 3.3% in stratum 10 to 5% in stratum 3. This gave, for mean densities of ringed seals, stratum error coefficients of variation between 7 and 20% — a good enough precision to show up differences between strata. The effectiveness of stratification can be assessed by comparing the clump factors C_1 and C_2. Both include small-scale clumpiness: the tendency of seals to occur in groups around holes or along cracks. If C_1 is of similar size to C_2, it shows a homogeneous stratum with transects varying randomly about the stratum mean, and little systematic east–west variation. If, on the other hand, a stratum could be subdivided into areas that were internally homogeneous, yet differed in density, or if there were continuous gradation in density across it so that adjacent transects were similar, while distant ones differed, C_2 would be much smaller than C_1.

The ratio C_1/C_2 was quite low for most strata — the median value was 1.31 in 1980 and 1.35 in 1981 — but there were one or two exceptions in both years (Table 5). In 1980, stratum 5 had a high ratio, because it could be split into a high-density area — Wellington Channel — and the remainder, which had a lower density; and in stratum 7, the eastern four transects, in Graham Moore Bay, showed uniformly higher densities than the ones in Byam and Austin channels (Table 6). The outstanding ratio in 1981 was in stratum 8, where there was a westward decline in density over the stratum (Table 6) and a first-order serial correlation of 0.85.

In both years, stratum 10 had high values for both clump factors, but their ratio was quite small. Stratum 1 had low ratios,



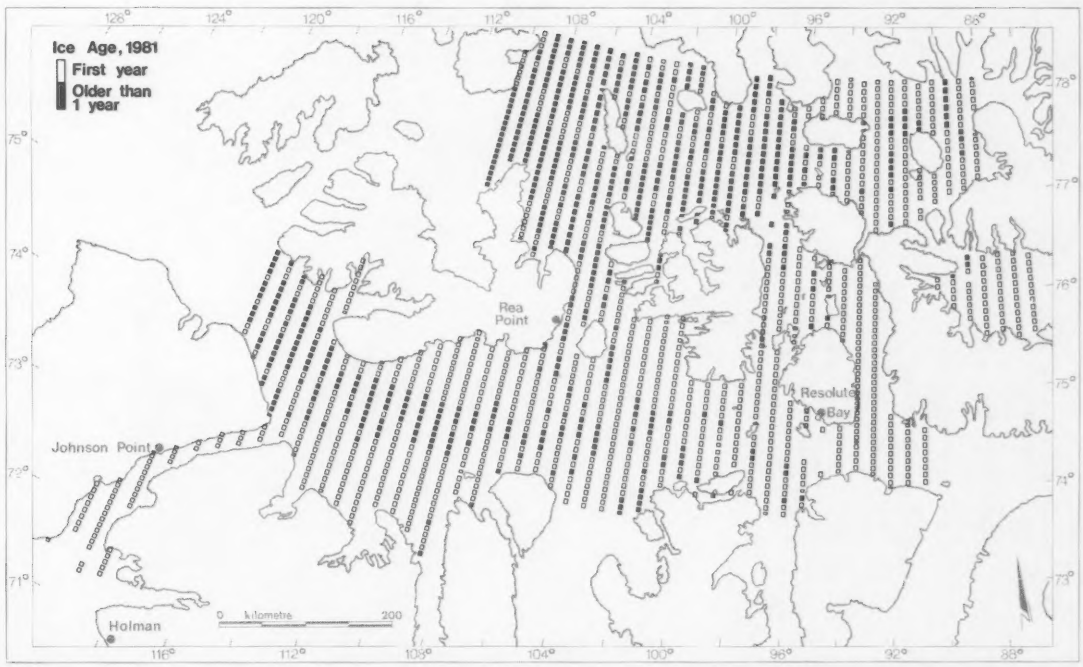


FIG. 2. Observations of ice age on transects, high Arctic seal survey.

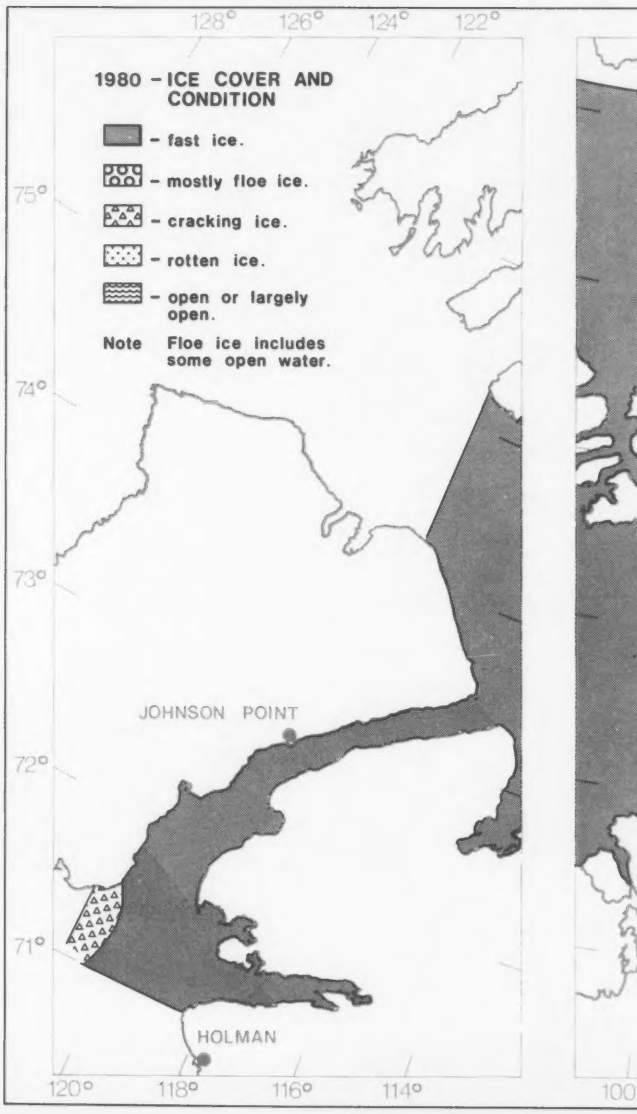
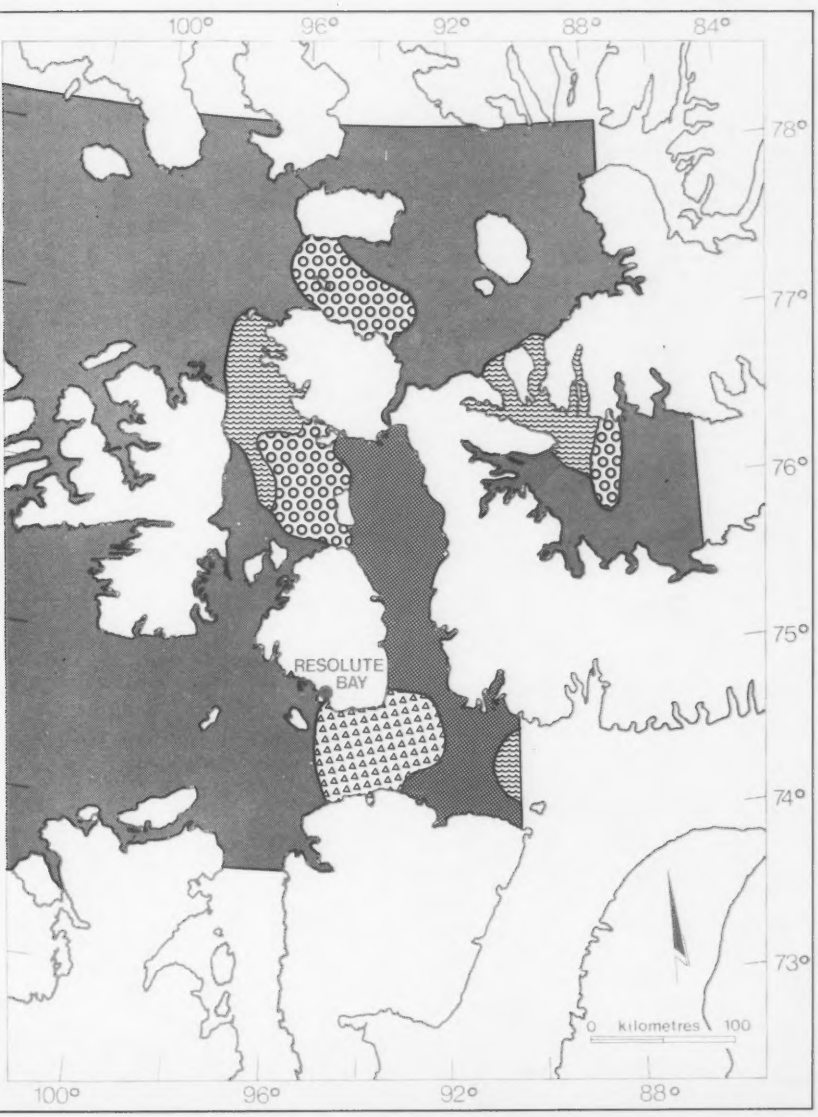


FIG. 3. Observations of open wa



f open water and ice conditions, high Arctic seal survey.

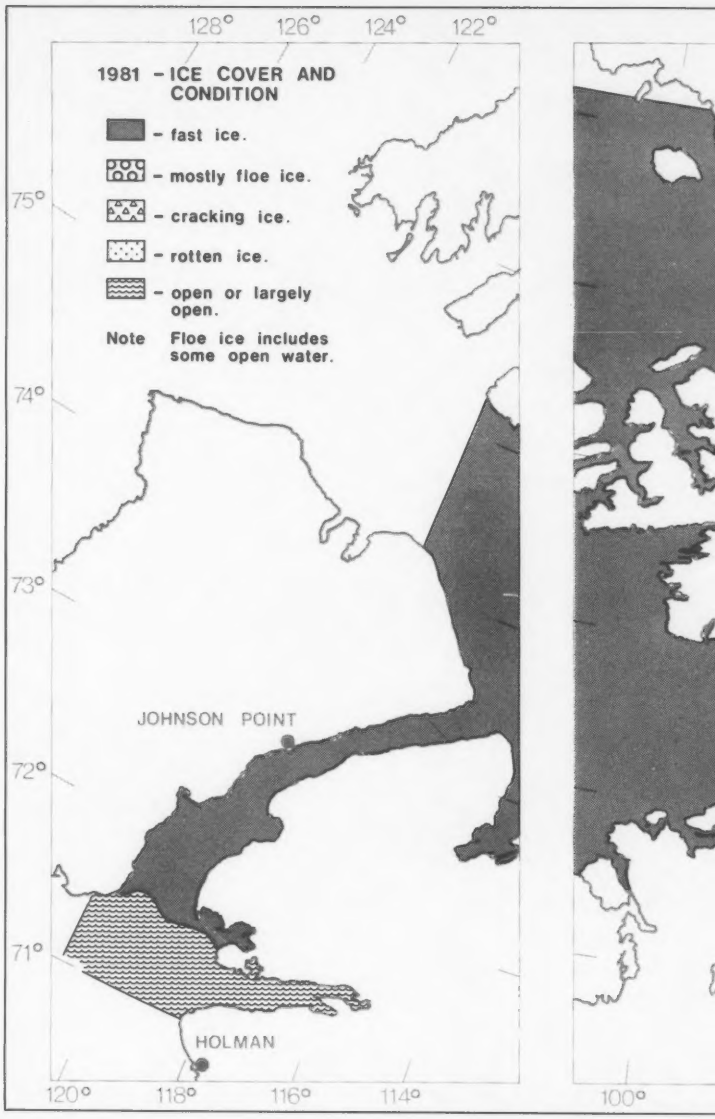
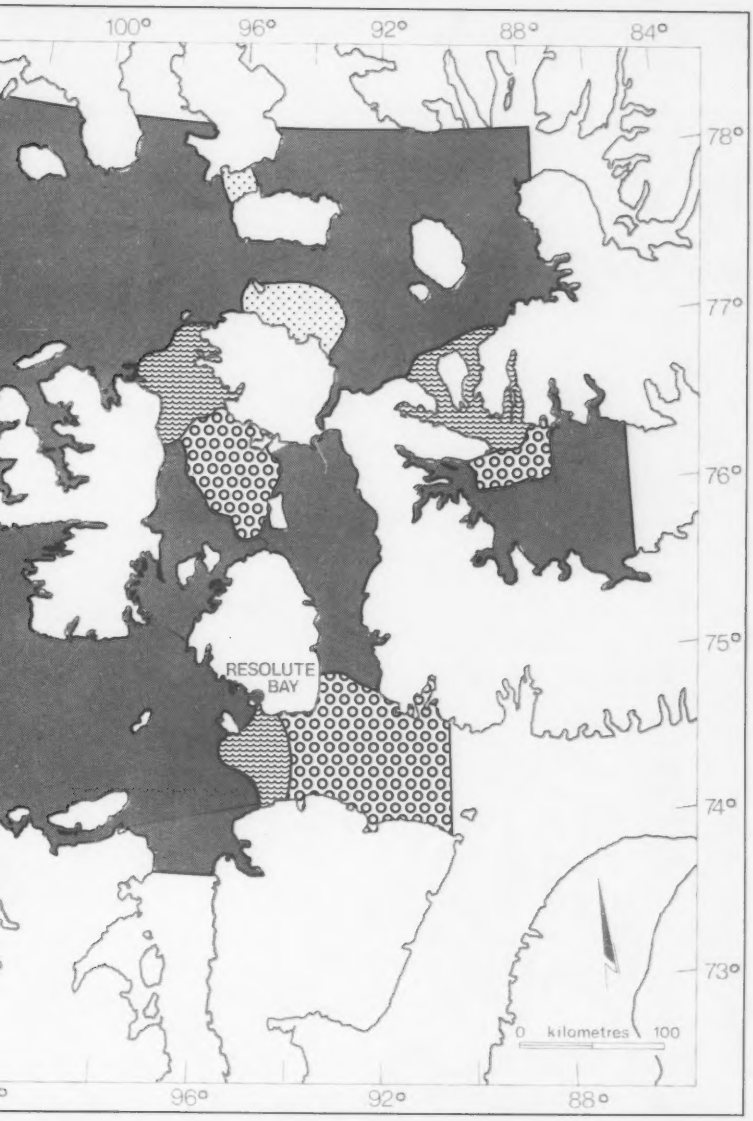

128°
126°
124°
122°
1981 – ICE COVER AND CONDITION
– fast ice.
– mostly floe ice.
– cracking ice.
– rotten ice.
– open or largely open.
Note Floe ice includes some open water.
75°
74°
73°
72°
71°
JOHNSON POINT
HOLMAN
120°
118°
116°
114°
100°

FIG. 3. (*Con*


100°
96°
92°
88°
84°
78°
77°
76°
75°
74°
73°
RESOLUTE BAY
0 kilometres 100
96°
92°
88°

3. (*Continued*)

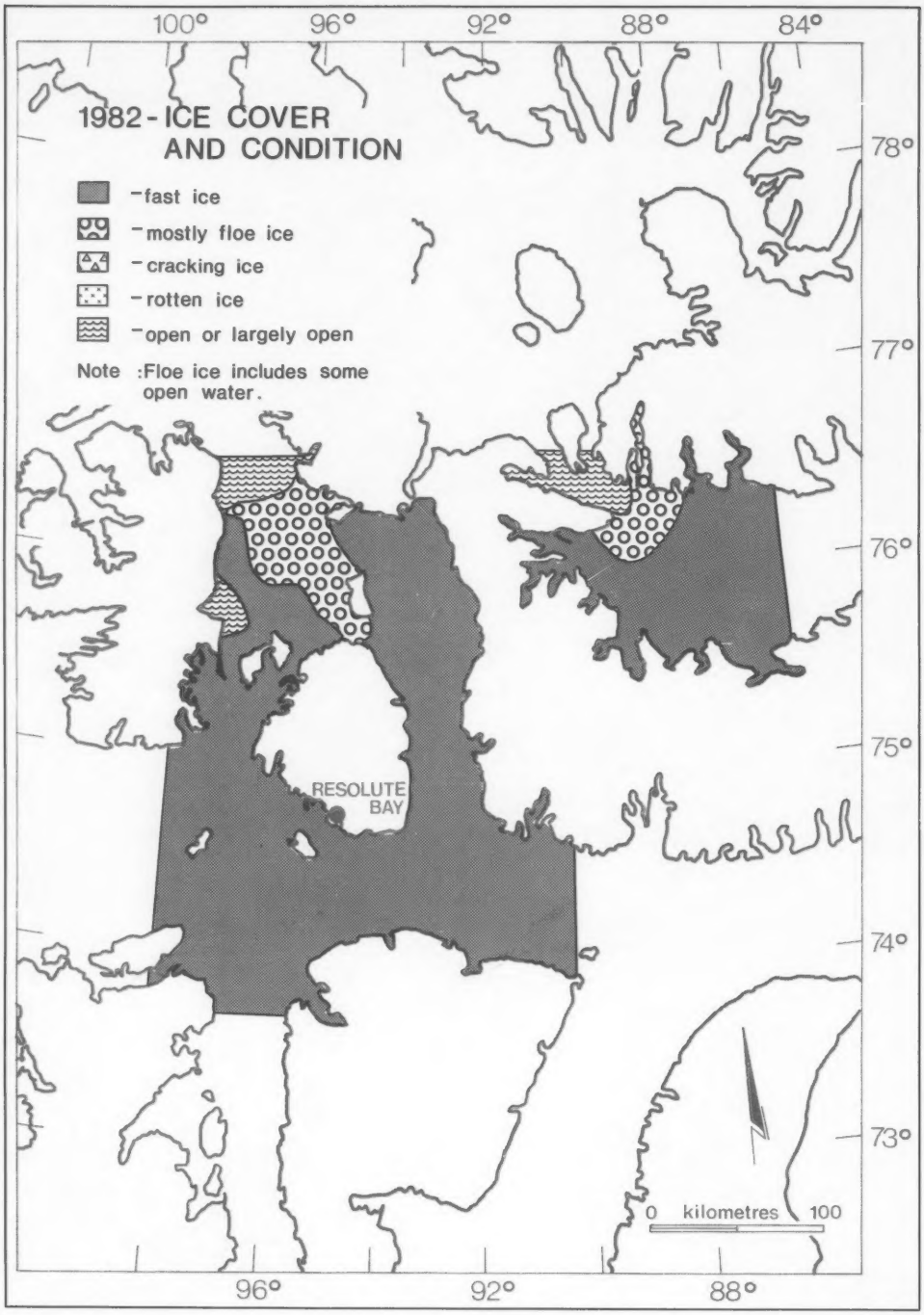


FIG. 3. (*Concluded*)

TABLE 3. Ice type percentage area (as a percentage of area with any ice cover) by stratum.

	Annual			Fast			Cracking			Floe			Rotten		
Stratum	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
1	97	96	73	75	72	91	8	3	0	13	10	9	3	14	3
2	31	82		84	74		3	1		8	2		4	23	
3	29	32		92	92		1	0		2	3		5	4	
4	0	27		100	100		0	0		0	0		0	0	
5	84	92	68	74	55	81	3	0	0	22	31	19	1	14	1
6	83	95	97	71	51	100	18	5	0	6	39	0	5	5	0
7	61	76		100	100		0	0		0	0		0	0	
8	36	73		100	100		0	0		0	0		0	0	
9	30	67		100	100		0	0		0	0		0	0	
10	94	100	100[a]	89	83	100[a]	10	5		2	12	0	0	0	0

[a]Includes "cracking."

TABLE 4. Ice cover percentage area by stratum.

		Open water			6/8+ cover			8/8 cover			Total ice surface		
Stratum	Area[a] (km^2)	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
1	9 660	11	7	6	80	82	88	70	79	82	82	85	89
2	24 044	1	2		90	92		82	78		93	92	
3	32 716	2	1		96	95		94	93		96	96	
4	29 806	0	0		100	100		100	100		100	100	
5	17 396	9	0	9	81	81	84	67	62	69	82	84	85
6	22 353	1	6	0	95	81	100	88	47	99	96	82	100
7	11 600	0	0		99	100		99	99		99	100	
8	31 687	0	0		100	100		98	100		100	100	
9	65 442	0	0		100	100		98	100		100	100	
10	13 041	0	34	0	98	57	100	75	41	100	95	58	100

[a]Total stratum area, including unflown transects, from 1980 data.

indicating a fortuitous alternation of high-density and low-density transects.

In 1980, the overall clump factor ratio was higher than that for any stratum; in 1981, it was exceeded only by that for stratum 8. This, with the generally low within-stratum values, showed that the stratification was effective, and that stratum boundaries were well placed.

Systematic sampling is effective in controlling sampling error in strata for which the clump factor ratio is high: we can be more confident that patches of high or low density have not been under- or over-sampled.

The repeatability of the survey was checked in 1980 by reflying transects in Amundsen Gulf on the way back to Inuvik at the end of the survey. The condition of the ice had changed by then, from mostly fast to mostly floe, and the density of seals had decreased (Table 7). The peak of haul-out had, also, probably passed at these lower latitudes. The standard errors of the densities were so large that the difference in density was not statistically significant.

In 1979, at the end of a seal survey in the Beaufort Sea (Stirling et al. 1982), four transects that had been flown earlier were reflown to check on the repeatability of the survey. The densities were different, but the changed ice conditions and the small sample size prevented the difference from being statistically significant (I. Stirling, unpubl. data). These experiences enable us to propose some conditions for useful reflying: (1) a short time interval, so that ice conditions are similar; (2) an adequate sample size; the differences looked for are such that a whole stratum should probably be reflown; (3) similar weather and times of day. Reflights so designed would estimate the error due to sampling in time.

TABLE 5. Clump factors and clump factor ratios for ringed seals (C_1 and C_2 calculated as in Methods; data used were for intervals with ice cover 6/8+ and no fog).

	C_1		C_2		C_1/C_2	
Stratum	1980	1981	1980	1981	1980	1981
1	4.77	4.12	6.67	5.60	0.72	0.74
2	4.32	2.86	4.22	2.92	1.02	0.98
3	6.69	4.03	3.87	3.28	1.73	1.23
4	2.04	3.12	1.73	2.07	1.18	1.51
5	16.57	4.79	5.39	2.32	3.07	2.06
6	14.34	45.90	7.56	25.46	1.90	1.80
7	8.13	7.08	3.38	5.13	2.41	1.38
8	5.93	15.03	4.26	2.45	1.39	6.13
9	5.87	3.78	6.36	2.86	0.92	1.32
10	18.37	74.89	15.06	59.59	1.22	1.26
2–4	6.18	9.34	3.65	3.20	1.69	2.92
5–9	33.00	37.75	9.30	12.93	3.55	2.92
1–10	36.04	70.27	11.11	26.12	3.24	2.69

Nonsampling errors tend to take the form of consistent biases, by their nature difficult to estimate, and controllable only by

TABLE 6. Transect densities (ringed seals/km^2) for strata with high clump factor ratios (selected data: 6/8+ ice cover and no fog; transects within each stratum are ordered from east to west).

Stratum 5, 1980		Stratum 7, 1980		Stratum 5, 1981		Stratum 8, 1981	
Transect	Density	Transect	Density	Transect	Density	Transect	Density
87	1.08	53	1.09	87	0.76	59	0.83
85	1.11	49	0.51	85	0.51	57	0.63
82	0.79	47	0.61	82	0.46	55	0.64
76	0.37	45	0.49	76	0.09	53	0.34
73	0.39	42–43	0.35	73	0.10	51	0.30
70	0.13	39–40	0.19	70	0.53	49	0.20
66–67	0.54	37	0.28	66–67	0.51	47	0.13
64	0.57	28	0.29	64	0.46	45	0.19
						42	0.25
						39	0.14
						36	0.29
Stratum mean density	0.75		0.48		0.51		0.33
C_1/C_2	3.07		2.41		2.06		6.13

TABLE 7. Ice conditions and ringed seal densities for four lines reflown in Amundsen Gulf in 1980.

	Ice cover percentage						
Date	6/8+	8/8	Annual[a]	Fast[a]	Cracking[a]	Floe[a]	Ringed seal density (seals/km^2)[b]
21 June 1980	98.2	70.9	98.4	87.0	11.2	1.8	0.861 (0.184)
9 July 1980	81.2	49.7	92.9	40.3	5.1	55.3	0.612 (0.247)

[a]As a percentage of area with any ice cover.
[b]Parenthesized values are standard errors.

TABLE 8. Comparisons of left and right observers and of inner and outer strips (selected data: 120-s duration and 6/8+ cover on both sides; no fog).

	Density (seals/km^2)				Error variances (10^{-4})			% difference		Student's t-test	
Year	Left	Right	Outer	Inner	V_w	V_s	σ_b^2	Left–right[a]	Outer–inner	Left–right	Outer–inner
1980	0.356	0.341	0.372	0.326	4.648	5.791	2.285	4.4	14.2	0.702	2.159[b]
1981	0.374	0.434	0.422	0.387	6.673	9.130	4.914	−16.0	9.1	−1.911	1.127

[a]As a percentage of the smaller value.
[b]Significant (two-tailed) at 5%.

careful surveying: but they may often be assumed constant over a survey, and therefore not to affect conclusions about relative densities in different areas. They include (1) visibility biases: not all seals living on a transect may be visible, and not all the visible ones may be seen and counted; (2) strip width errors: strut or window marks may not be placed quite right, and the width of the strips increases when the aircraft banks to correct or maintain its course on transect and decreases when the aircraft crabs in a crosswind, and is directly affected by altitude error.

Altitude error was controlled in 1981 by using a radar altimeter. In 1980 we used a pressure altimeter, and were often flying far from the nearest weather station from which corrections could be obtained. However, we were usually in large, stable weather systems — because such systems give good survey conditions — and do not think this was a serious source of error.

At any time, some seals are under the ice and therefore cannot be seen. The greatest numbers haul out on the sea ice during early to mid-afternoon (Smith 1973a; Finley 1979; Smith and Hammill 1981). The maximum proportion hauled out has been estimated at 50% (McLaren 1958a;Smith 1973a), at 70% or more (Finley 1979), and at 80% (Smith and Hammill 1981). We minimized the effect of daily variation in the pattern of haul-out by flying as much as possible during the middle of the day.

Other nonsampling errors were checked by comparing densities obtained in the inner and ounter strips, and by the left and right observers (Table 8). In surveys of camouflaged terrestrial mammals (Caughley 1974), visibility has been found to decrease with distance from the aircraft. In contrast, we recorded higher densities in the outer strips in both years, by 14% in 1980 and by 9% in 1981. Seal surveys, flown using the same methods, in the Beaufort Sea had found the same thing (Stirling et al. 1977;

Stirling et al. 1982). There are several possible causes for these unusual results: (1) seals near the aircraft may have been more likely to dive as the aircraft approached, and so not to be recorded; some certainly did; (2) seals near the aircraft were more briefly in sight than seals further out, and more apt to be missed; (3) the observers may have found it easier to look outward than downward; (4) the outer strip was more apt to be widened when the aircraft banked to correct its course; even flying on autopilot, small corrections were necessary; (5) observers may have been less sure of the outer edge of the outer strip, because of the flat viewing angle (20°), and been apt to include doubtful seals.

In 1980 the two sides differed in mean density by only 4.5%. In 1981 the difference was 16%, but varied greatly between strata and was not statistically significant.

Ringed Seal Habitat Regressions

Multivariate regression has been used before on wide-area survey data (e.g. Finley 1976; Bradstreet and Finley 1977) to try to study effects of weather on the presence or visibility of animals, but sometimes with poor results. We ran four sets of regressions.

The first was intended to elicit a critical ice cover level for ringed seals and offered ice cover, depth, weather, and time variables. The results (Table 9) showed a 6/8 cutoff point for the 1980 data, and 8/8 for 1981. We decided from this to consider 6/8+ ice cover as ringed seal habitat, and further regressions, and calculations of stratum densities, were carried out on data so selected. The ignoring of 1/8 to 5/8 ice cover is not serious; it constitutes only about 4% of the total area although a larger proportion of the most productive strata (up to 19% of stratum 5 in 1981) (Table 4). In 1980, 5 of 3904 ringed seals were counted on 1/8 to 5/8 ice cover. In 1981, the overall proportion was higher — 98 of 4007. Of these 98, 81 were in stratum 10 and were seals counted in high density behind the fast-ice edge in intervals that had short durations over the ice, and therefore recorded low average cover. Another large coefficient in the 1980 data was a negative one for "anyfog." Fog and rain variables had negative effects on densities, so data from foggy and rainy days were not used in subsequent analyses.

The second set of regressions used selected data — 6/8+ ice cover and no fog or rain — and offered variables for weather (cloud cover and wind speed), water depth, sun time, and ice type. The results (Table 10) were inconsistent, and the weather and sun time coefficients were difficult to interpret. The 1980 data showed a negative coefficient for suntime >10:00 as well as for suntime >15:00; and the 1980 results had a high positive coefficient for strong winds (wind 3+). These results were inconsistent with current knowledge of the haul-out behaviour and preferences of ringed seals (Finley 1979), and we suspected that some of the weather variables, with their anomalous-seeming and possibly spurious coefficients, were affecting the entry of habitat variables.

We concluded that multivariate regression using these wide-area survey data was ineffective for analyzing fine effects of weather on haul-out behaviour and ran a third set of regressions offering only ice age, ice condition, and depth variables, and this (Table 11) produced some clear indications of preferred habitat types, consistent between years and with existing information. Results for 1980 showed preferences for annual ice, and for a depth band from 50 to 175 m (classes 3–6). Rotten ice was disliked. For 1981, the same upper limit of preferred depth emerged with preferences for annual and fast or cracking ice.

TABLE 9. Variables entering habitat regressions for ringed seals when ice cover, water depth, weather, and time variables were offered for all data from flown transects (all data for flown transects included; ice type variables not offered; standard errors given in parentheses).

Variable	Coefficient (seals/km^2)	
	1980	1981
6/8+ cover	0.438 (0.045)	
8/8 ice cover		0.341 (0.040)
Depth >50 m	0.156 (0.036)	
Depth >125 m		−0.212 (0.049)
Depth >150 m	−0.136 (0.033)	
Depth >175 m	−0.127 (0.035)	−0.177 (0.054)
wind2p	−0.072 (0.024)	
wind3p		0.447 (0.048)
anyfog	−0.223 (0.039)	
stgt10	−0.162 (0.044)	
stgt12	−0.110 (0.039)	
st13[a]	−0.034 (0.006)	
st13sq[a]		0.022 (0.003)
Coefficient of determination (%)	13.8	11.5

[a]Continuous variables in hours; others are binary.

TABLE 10. Variables entering habitat regressions for ringed seals when ice cover, ice type, water depth, weather, and time variables were offered for selected data: 6/8+ ice cover and no fog or rain (standard errors given in parentheses).

Variable	Coefficient (seals/km^2)	
	1980	1981
Constant[a]	0.678 (0.058)	
Depth >125 m		−0.262 (0.046)
Depth >175 m	−0.216 (0.032)	
Annual	0.268 (0.029)	0.181 (0.043)
Fast		0.222 (0.050)
Cracking		1.868 (0.026)
Large floe	−0.382 (0.128)	
Rotten	−0.394 (0.122)	
Scatplus	−0.084 (0.028)	
wind3p		0.440 (0.053)
stgt10	−0.309 (0.058)	
stgt15	−0.094 (0.030)	
st13sq[b]		
Coefficient of determination (%)	13.7	15.6

[a]An optional constant was offered in all regressions.
[b]Continuous variables in h^2; all others are binary.

The residual error from this set of regressions was regressed against a family of binary variables corresponding to the strata. Table 12 shows that in both years, strata 6 and 10 had high densities not attributable to their ice habitat types. In 1980, stratum 5 also had higher densities than would have been predicted from its habitat, but not in 1981. The density in stratum 1 was lower in 1980 than would have been expected from its annual ice, even allowing for its deep water. In 1981, strata 2 and 4 had negative effects, that is, lower densities of

TABLE 11. Variables entering habitat regressions for ringed seals when ice type and water depth variables were offered for selected data: 6/8+ ice cover and no fog or rain (standard errors given in parentheses).

Variable	Coefficient (seals/km^2) 1980	1981
Constant	0.192 (0.042)	
Annual	0.254 (0.028)	0.263 (0.043)
Fast		0.363 (0.046)
Cracking		2.350 (0.261)
Rotten	−0.364 (0.115)	
Depth >50 m	0.171 (0.045)	
Depth >150 m	−0.122 (0.038)	−0.283 (0.046)
Depth >175 m	−0.177 (0.040)	
Coefficient of determination (%)	12.0	9.5

TABLE 12. Stratum binary variables entering regressions of ringed seal density residuals from Table 11 (standard errors given in parentheses).

Stratum	Coefficient (seals/km^2) 1980	1981
1	−0.244 (0.068)	
2		−0.193 (0.065)
4		−0.168 (0.055)
5	0.226 (0.050)	
6	0.262 (0.045)	0.635 (0.083)
10	0.202 (0.062)	1.345 (0.124)
Coefficient of determination (%)	5.4	11.2

seals than would have been predicted from ice type and depth. They both had low densities of seals in both years, but in 1981 (because of extensive breakup in 1980) both had higher proportions of annual ice. However, seal density had not increased in response to this change.

Within the high-cover habitat preferred by ringed seals, small-floe ice was rare and most of the ice, at survey time, was fast. Cracking, large-floe, and rotten conditions all tended to be associated with annual age, and of these, cracking was preferred and the other two shunned. To summarize: in fast-ice areas, annual ice had a higher density of seals than multiyear; in annual-ice areas, cracking ice had the highest densities, followed by fast ice, and floe and rotten ice had lower densities. We noticed when flying surveys that ringed seals hauled out at holes and along the edges of narrow cracks in fast and cracking ice, but almost never on the edges of wide cracks, leads or floes; they were occasionally seen at cracks or holes in the middle of the very largest floes.

These results corresponded with previously established preferences (McLaren 1958a; Smith 1973b) of ringed seals for landfast ice. The preference we found for "cracking" ice may have several bases. The first is that this ice condition typically occurs behind ice edges, and these high densities may reflect an incipient collapse of the winter underwater social structure, with seals opportunistically hauling out at newly available sites. Another possibility is that these large numbers of seals had moved in from areas where the ice had already disappeared to take advantage either of newly available haul-out sites or of feeding areas. The cracking ice behind ice edges may provide good foraging for ringed seals. The Arctic cod (*Boreogadus saida*) apparently schools under ice (Sekerak and Richardson 1978), and ringed seals may have a source of food with less competition from seabirds than at the ice edge, breathing places without infringing on other seals' breathing holes, and dry haul-out sites on the well-drained crack edges. Similar movements have been recorded for Weddell seals (*Leptonychotes weddelli*) in the same season and habitat, and have been attributed to the use of feeding areas newly available as the fast ice cracks ahead of the ice edge (Stirling 1969).

We found few consistent and interpretable responses to cloud cover, wind speed, or time of day. We did find for the 1980 data that densities were reduced by fog. In 1981, similar effects for both fog and rain occurred, but were not statistically significant, because fog and rain were rare. Apart from fog, we had a good range of cloud covers, and one, "scattered or heavier" entered for 1980 with a negative coefficient.

Analysis of density in terms of wind speed and time of day suffered from the fact that, to get good counts, we tended to fly at the optima of both. In 1981, the wind speeds recorded were mostly in class 2, but in both years, we found it difficult to estimate wind speed when flying over fast ice, and in 1980 many data values were missed. Wind speeds appeared in regressions for both years, but with conflicting signs.

Data from studies of the haul-out behaviour of polar seals shows that they have a band of preferred weather conditions, and may retreat to the water if it is too calm and sunny (Harrison and Kooyman 1968; Burns and Harbo 1972; Øritsland and Ronald 1978; Finley 1979) or remain there if it is windy (Smith 1965; Smith 1973a; Finley 1979). Smith and Hammill (1981) found wind speed to be inversely associated with numbers of hauled-out ringed seals.

There is good evidence for a daily cycle of haul out in ringed seals (Smith 1973a; Finley 1979), especially early in the season (Smith and Hammill 1981), with a peak from midday to early afternoon. We would therefore have predicted our regressions to produce positive coefficients for "sun time > 9:00," "sun time > 10:00," or "sun time > 11:00" and negative ones for, say, "sun time > 16:00" or "sun time > 17:00." None of these binary variables entered, however, and this lack of a clear result is probably because we surveyed as much as possible during the middle of the day and did not obtain comparative values from other times.

Smith (1973a) and Finley (1976) also used multiple regression to try to elucidate, from survey data, the weather preferences of ringed seals for hauling out. Smith (1973a) obtained negative association with cloud cover and wind; Finley (1976) obtained positive coefficients for cloud cover and temperature (a preference for warm cloudy weather) and, like us, failed to find effects for wind speed or time of day.

Ringed Seal Densities

The habitat regressions identified high ice cover areas as being favourable seal habitat. The 1980 cut-off point was at 6/8, and that for 1981 was 8/8. The 1980 results also showed that a significantly lower density of seals was counted in fog. Inspection of the 1981 regressions also showed that rain tended to depress densities, although for 1981 neither fog nor rain had statistically significant effects, both being too rare. With these factors in mind, stratum mean densities were calculated for both years using data selected for 6/8+ ice cover and no fog or rain.

The density estimates (Table 13) appeared to divide the strata into three classes. In the lowest class of density were strata 2, 3, 4, and 9. Strata 2–4 receive cold, probably nutrient-poor water from the Arctic Ocean, and they are covered largely by multiyear ice which breaks up little and late, so they receive less solar warming or enrichment, and they are generally biologically unproductive. Stratum 9 also has much multiyear ice, and is deep.

Stratum 2 is anomalous in this class. It is not so deep as the others, and although in 1980 it had 80% multiyear ice, in 1981 it was mostly annual ice and was already starting to show some open water at survey time; Smith et al. (1979; Fig. 2) also found mostly annual ice there. In habitat terms, stratum 2 shows affinities to stratum 7, also shallow with currents which sometimes cause small polynyas and early opening, and a mix of annual and multiyear ice. However, the densities in stratum 7 are double those in stratum 2, and reasons for this difference are not apparent. It may be related to the greater proportion of fast annual ice, preferred by ringed seals, in stratum 7. Smith et al. (1979) found that densities of ringed seals decreased as latitude increased in the interisland channels north of Resolute. This trend may be related to increasing proportions of multiyear ice in those areas.

In the middle class with stratum 7 were strata 8 and 1. Stratum 8 is similar to stratum 7 in location, in depth, and in the existence of shallow and early-opening areas around islands and off points of land; both strata tend toward annual ice, with multiyear ice occurring as floes refrozen into it. It was, therefore, not surprising that they should be so similar in density. Of this class, stratum 1 is the oddity. It shows many similarities to strata 5 and 6: situated between the North Water and recurring polynyas near the Grinnell Peninsula; early open water; and mostly annual ice. However, its densities were much lower, and we suspect two principal reasons for this: most of it is much deeper than ringed seals prefer, and there is a substantial wintering population of walruses. Male walruses in particular are known to eat ringed seals (Loughrey 1959; Fay 1960; Lowry and Fay 1984), and it is regarded as common knowledge by Inuk seal hunters that ringed seals avoid walruses. Even within stratum 5, there is a high-density area for ringed seals (Wellington Channel) and a lower-density area which, like western Jones Sound, is a wintering area for walruses. The presence of walruses may contribute to the lower density of ringed seals in stratum 1.

Strata 5 and 6 are, with stratum 10, the highest-density strata. All three are completely covered with annual ice, but open regularly, early, and by cracking back from stable ice edges. They are near recurring winter polynyas. Currents in Lancaster Sound flow west along the south coast of Devon Island into Barrow Strait and north along the east coast of Wellington Channel, where they mix with water that has passed through the polynyas of Penny Strait and Queens Channel. There is also mixing with the main eastward current through Barrow Strait, and this mixing of waters and nutrients may increase biological productivity and raise densities of ringed seals.

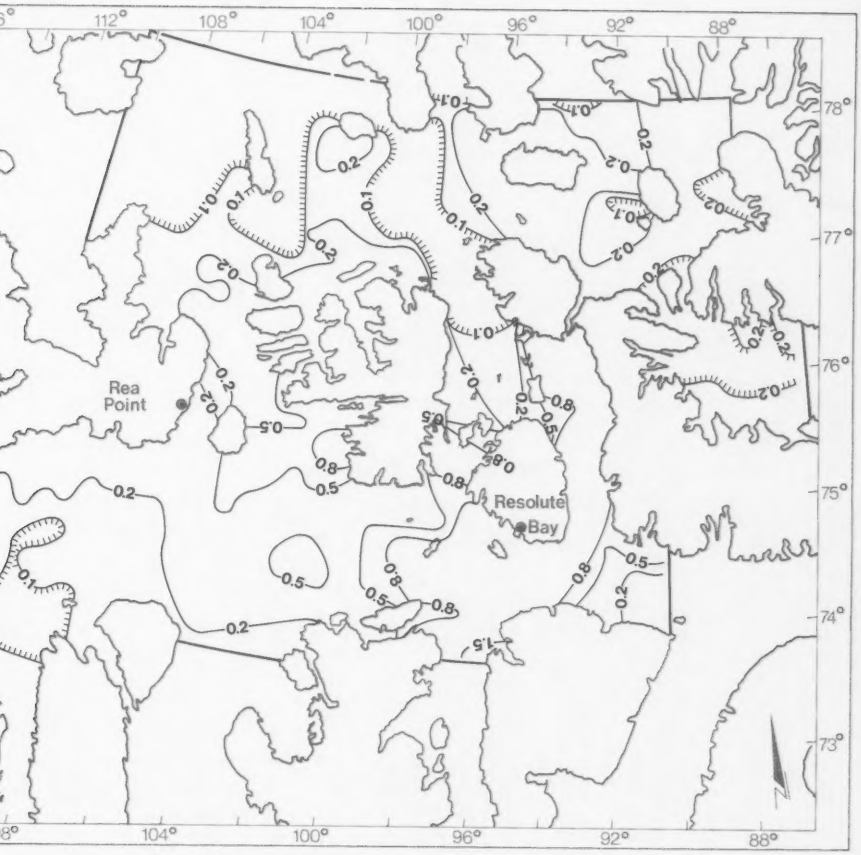
Part of the reason for the high densities at survey time in these strata is that the cracking zone behind an ice edge offers good habitat for seals which have wintered in areas that open before the survey. The "cracking" ice type is shown by regression results to be preferred. It offers a dry, stable habitat to haul out on and, more important, access to feeding and breathing sites.

Previous studies of the distribution of breeding ringed seals have stressed the importance of stable landfast ice in bays and

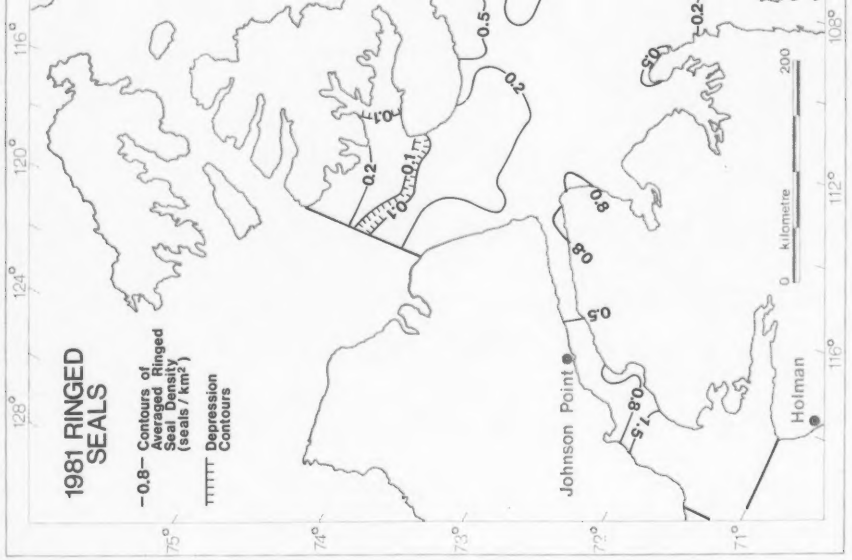
TABLE 13. Densities of ringed seals by stratum (data used were from intervals with 6/8+ ice cover and no fog; standard errors given in parentheses).

Stratum	Density (seals/km^2)			Rank		Estimated population (10^3)			No. of transect lines flown		
	1980	1981	1982	1980	1981	1980	1981	1982	1980	1981	1982
1	0.2402 (0.0681)	0.4314 (0.0973)	0.3260 (0.0770)	7	4	1.87 (0.53)	3.50 (0.79)	3.15 (0.74)	7	7	7
2	0.2520 (0.0339)	0.1931 (0.0226)		6	9	5.47 (0.74)	4.32 (0.51)		12	12	
3	0.1733 (0.0238)	0.2487 (0.0240)		9	8	5.42 (0.74)	7.81 (0.75)		12	13	
4	0.1067 (0.0140)	0.0600 (0.0096)		10	10	3.18 (0.42)	1.79 (0.29)		9	9	
5	0.7471 (0.0810)	0.5129 (0.0456)	0.6000 (0.1170)	3	3	10.53 (1.14)	7.16 (0.64)	10.44 (2.03)	8	8	3
6	0.8518 (0.0884)	1.1576 (0.2079)	0.9000 (0.0820)	1	2	18.08 (1.88)	21.07 (3.78)	20.12 (1.83)	12	11	12
7	0.4794 (0.0635)	0.4111 (0.0654)		4	5	5.49 (0.73)	4.77 (0.76)		8	9	
8	0.3583 (0.0353)	0.3292 (0.0250)		5	6	11.35 (1.12)	10.57 (0.80)		11	11	
9	0.2071 (0.0226)	0.3157 (0.0190)		8	7	13.52 (1.48)	20.61 (1.24)		18	18	
10	0.7631 (0.1615)	2.2304 (0.7168)		2	1	9.80 (2.07)	16.54 (5.32)		8	8	
2–4						14.07 (1.13)	13.92 (0.95)				
5–9						58.97 (2.97)	64.18 (4.18)				
1–10						84.71 (3.83)	98.14 (6.88)				

FIG. 4. Locally averag



averaged ringed seal density, high Arctic seal survey.


1981 RINGED SEALS
–0.8– Contours of Averaged Ringed Seal Density (seals / km²)
Depression Contours
Johnson Point
Holman
0 kilometre 200
128°
124°
120°
116°
112°
108°
75°
74°
73°
72°
71°

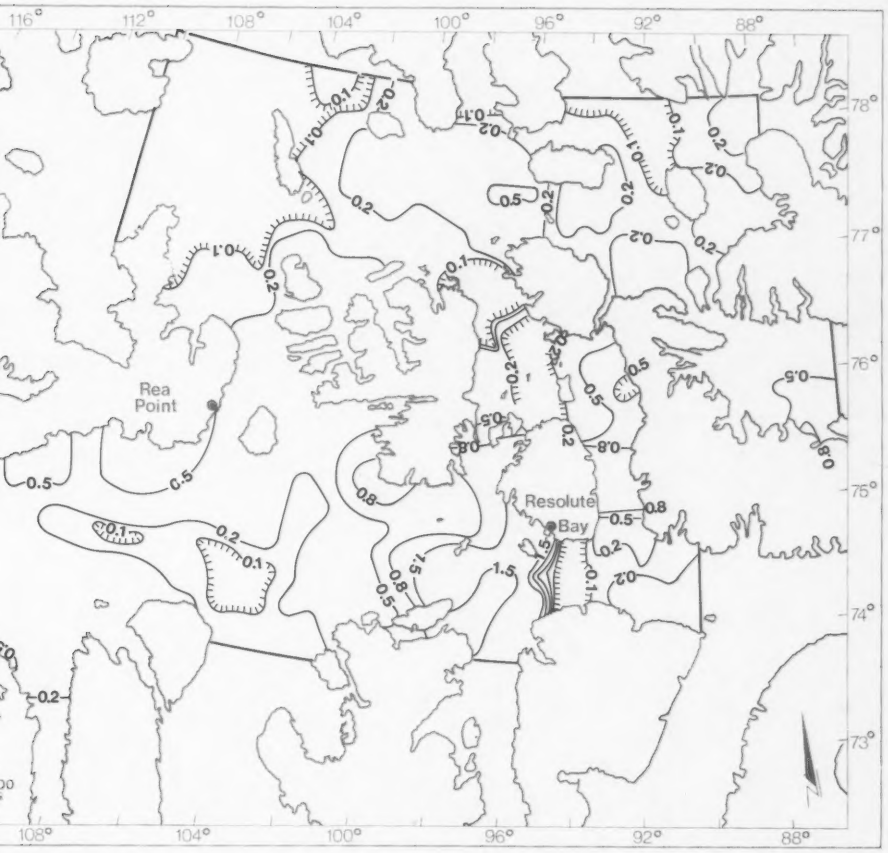


FIG. 4. (*Continued*)

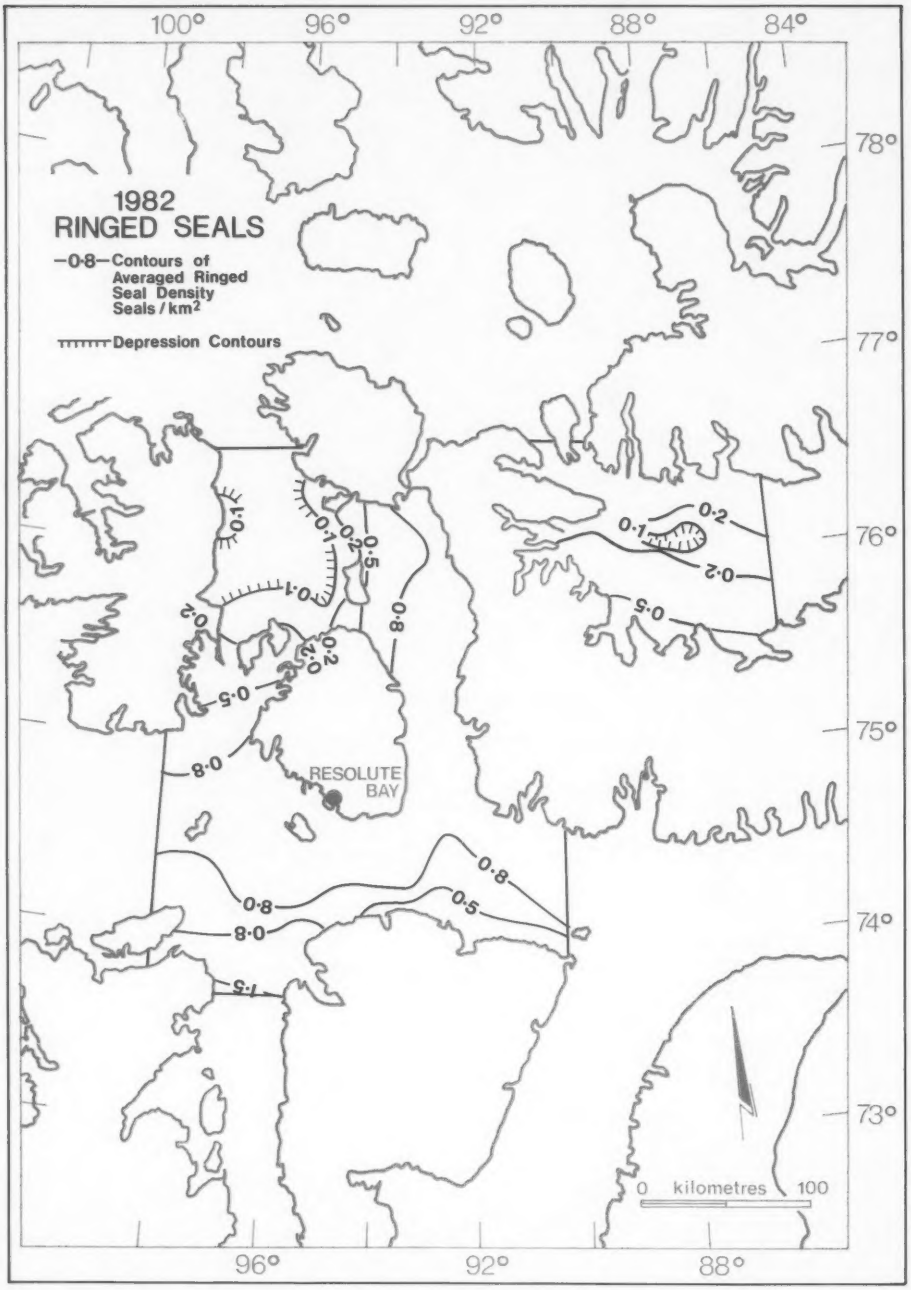


FIG. 4. (*Concluded*)

near coastlines (McLaren 1958a) in areas such as southern and southeastern Baffin Island where offshore ice tends to be mobile and unstable. Following those studies, the first surveys of the distribution of ringed seals in the high Arctic continued to compare densities in areas arbitrarily defined as being "nearshore" and "offshore." Finley (1976) and Smith et al. (1978) surveyed parts of our strata 5–8 but found no significant differences between the nearshore and the offshore areas (though both found, as we did, high densities in Aston Bay). In the high Arctic, snowfall is low, so smooth bay ice has little snow cover; however, the offshore ice, locked in interisland channels, is stable. In preliminary surveys of ringed seal birth lair habitat in the high Arctic, T. G. Smith and I. Stirling (unpubl. results, cited in Stirling et al. 1981) found little snow

TABLE 14. Densities (seals/km^2) of ringed seals in the high Arctic from this and other surveys.

Stratum	This survey 1980	1981	1982	Smith et al. (1978)[a]	Finley (1976)[b]	Smith et al. (1979)
2 + 3	0.21	0.22				0.29[c]
5	0.75	0.51	0.60	0.47	0.84–1.54[d]	0.49[e]
6	0.85	1.16	0.90	0.73	0.58–0.85	
7	0.48	0.41		0.24	0.62–0.82	
8	0.36	0.33		0.59	0.79–0.85	

[a]Weighted mean of values from Smith et al. (1978, tables 4 and 5).
[b]As reported by Smith et al. (1978, tables 4 and 5).
[c]Weighted mean density of lines 75°N to 76°30′N from Smith et al. (1979, table 1).
[d]Wellington Channel only.
[e]Weighted mean density of lines 76°30′N to 78°30′N from Smith et al. (1979, table 1).

cover and few breeding seals in the bays. Birth lairs were more abundant in the drifted pressure ridges across the mouths of bays and in the interisland channels such as western Barrow Strait, and these areas may be very important as breeding habitat to ringed seals in the high Arctic. Thus, it appears that throughout much of the archipelago, where fast ice can be firmly locked between the islands, the densities of ringed seals are best evaluated on the basis of local conditions such as ice age, ice condition, and depth of water.

The surveys mentioned above, and that of Smith et al. (1979), for ringed seals in the high Arctic, gave similar results to ours (Table 14). The higher densities obtained for stratum 8 by both Smith et al. (1978) and Finley (1976) are due to their surveys' being weighted toward the higher-density eastern end of the stratum.

The most significant conclusion we can draw from the results within our survey area is a general division between the western and northwestern multiyear-ice areas, and the annual-ice areas to the east and southeast (Fig. 4). On this basis, the ecotone between the unproductive sparsely populated areas of strata 4 and 9 and the west end of stratum 3, and the productive areas of strata 5 and 6 and the east end of stratum 8, lies along the western end of stratum 8, stratum 7, and the eastern end of stratum 3.

Densities of Seal Holes

The counting of seal holes is a useful adjunct to seal counts obtained in aerial surveys. For one thing, it provides a more stable measure of density: seal holes cannot dive when an aircraft approaches, nor do they show short-term responses to the weather as seals are believed to. Furthermore, they are immobile and show the relative winter density of seals (Alliston and McLaren 1981), rather than the density at survey time, when seals may already have started to move about as ice conditions change. Digby (1983) described initial tests of side-looking airborne radar, aerial photography, and satellite imagery to detect seal breathing holes. She suggested that remote sensing of the drained ice around seal holes may in future be used to estimate densities of wintering seals.

There are, however, a number of difficulties associated with recording seal breathing holes visually from aircraft. They are not always visible, and observers may vary in their ability or willingness to record seal holes inferred from such clues as drainage patterns, depressions in snowdrifts, or concentrations of polar bear tracks; in comparison, seals are easy to be sure of. This problem may be overcome with increasing experience and the establishment of rules for recording holes. Seal holes may be hidden by rafted ice or covered with snow, so their visibility often varies with ice type and may change with time as snowmelt proceeds. In mosaics of first-year and multiyear ice, for example, the first-year ice may be bare of snow and completely flooded, except for residual snowdrifts at the edges of the multiyear floes — the preferred location for seal holes in this kind of ice. Another example is given by Alliston (1980): he recorded an overnight threefold increase in the apparent density of seal holes in the Beaufort Sea, which he ascribed to rapid melting of the covering snow in warm weather, with a consequent increase in detectability.

To draw firm conclusions from seal hole counts, it is necessary to assume that each winter resident seal uses about the same number of holes in any kind of ice and whether the seal density is high or low; it is not known whether this is so. We noticed when flying the surveys that strings of holes are often maintained along refrozen cracks, so ice that cracks and refreezes in winter may have higher hole densities than more stable ice, irrespective of seal density.

When we analyzed the results from the 1980 survey and found the low seal densities we did in some areas, we thought we remembered seeing few seal holes there, but in the absence of a record, we could not be sure. Therefore, in 1981 and in 1982 we recorded seal holes, but only in fast ice.

In 1981, both observers recorded holes in both inner and outer strips. The densities obtained by the two observers were, overall, quite close for the inner strips. One observer recorded similar densities in the outer strip as well, but the other had been more conservative in inferring holes in the outer strip and obtained much lower densities. Consequently, we used only inner-strip data in the analyses. The results for the 1981 survey and the 1982 partial resurvey (Table 15) show a weak association between seal densities and seal hole densities. Stratum 4 stands out clearly with low densities of both; strata 6 and 10 in 1981 are anomalous, since we think that there were local increases in seal density owing to the early breakup in these strata; and the remaining strata show a weak positive association.

Bearded Seal Densities and Habitat Preferences

Bearded seals were much less abundant in the study area than ringed seals, and largely absent from the tracts of multiyear ice

FIG. 5. Observations o

tions of bearded seals, high Arctic seal survey.

TABLE 15. Densities of seal holes by stratum, high Arctic survey area (standard errors given in parentheses).

Stratum	Seal hole density (holes/km^2) 1981	1982	1981 rank Hole density	1981 rank Seal density
1	5.11 (0.58)	5.05 (0.36)	2	2
2	2.80 (0.33)		3	7
3	1.80 (0.12)		4	6
4	0.15 (0.05)		8	8
5	5.54 (0.43)	4.08 (0.41)	1	1
6	4.42 (0.36)	4.85 (0.27)	[a]	[a]
7	1.65 (0.21)		5	3
8	1.54 (0.15)		7	4
9	1.56 (0.17)		6	5
10	3.46 (0.25)	3.60 (0.18)	—[a]	—[a]
			Spearman's $r = 0.60$	

[a]These strata were not ranked, since it seemed that their 1981 seal densities were partly due to early breakup; if they are included, Spearman's $r = 0.68$.

in strata 4 and 9 (Fig. 5). A survey to estimate accurately the densities of bearded seals would need to be much denser, and concentrate on the other strata. The observations we obtained were, however, enough to make some tentative deductions about bearded seal habitat preferences by examining two-way contingency tables of the presence or absence of bearded seals against habitat factors. Bearded seals preferred broken ice — fast ice had fewer than expected in both years — with, apparently, the greatest preferences for large floes and rotten ice. The cover range preferred was the 6/8 to 7/8 range, with fewer seals than expected in 8/8 cover; annual ice was also preferred. In 1981, preferences appeared for water depths less than 100 m, with the strongest for those between 25 and 50 m; in 1980, depths of 50–100 m were preferred. In both years, water deeper than 100 m had fewer bearded seals than would be expected from its frequency. Shallower water tends to be associated with moderate cover and with floe and rotten ice. A preferred habitat type from these results for bearded seals would thus be floe or rotten annual ice of moderate cover over shallow water.

Burns et al. (1980) associated bearded seals in the Bering Sea with "open pack," "flaw," and "front" zones, where ice cover is less than 7/8. Burns and Frost (1979) associated bearded seals in winter with shallow water in "flaw" zones, over the northern part of the Bering Sea shelf, and in summer, with the overlap of the pack-ice front and the western Beaufort and Chukchi shelves. They reported that bearded seals were not associated with the ice front when it receded to deep water in good summers. Burns (1967) noted that bearded seals moved away from the shallowest coastal water in fall as fast ice formed and was inhabited by ringed seals.

Within the annual-ice area, we found only a very weak (−0.017) negative correlation between ringed and bearded seal densities; with the rather different habitat preferences, we expected it to be stronger.

Conclusions

In the Canadian high Arctic area covered by this survey, the densities of ringed seals declined to the north and west. This decline is associated with, but not wholly explained by, an increase in the amount of multiyear ice from almost none at the southeastern limit of the survey to 100% at the northwestern limit.

Ringed seals preferred fast or cracking ice of high cover to haul out on, and were found in high densities behind fast-ice edges; they were seldom seen hauled out on floe ice. Their observed distribution was affected by the availability of suitable haul-out habitat, and surveys should be timed to ensure good cover of fast ice. Multiple regression showed no consistent effects of weather or time of day, but did show a tendency for ringed seals to avoid the deepest water. The whole survey was repeated only once, and showed no major fluctuations in estimated populations of ringed seals; however, these are too few data on which to base conclusions about the stability or otherwise of high Arctic ringed seal populations.

The survey was not well designed to describe accurately the distribution of bearded seals: it was too sparse, and spent too much time over fast ice. They were seen in much smaller numbers than ringed seals in a small part of the survey area. The areas where they were seen were characterized by partial cover of floe ice, where currents and shallow water caused early thinning and breakup of the ice cover. In 1982, an early ice year, we saw the most bearded seals; in 1983, a late ice year, we saw none; and 1981 was intermediate in both respects. This may show that bearded seal counts at this time are affected by their movement into fast-ice areas from wintering areas elsewhere.

Some future work is suggested by the results of this survey. There is clearly a requirement to develop a technique for estimating winter distribution of seals, and to find out why Jones Sound has many seal holes but few surveyable seals. We should like to know whether there is a short-term response of seals to annual ice when it occurs in areas that usually have multiyear ice. Further behavioural studies are needed to estimate the visibility bias due to seals' being under the ice, and to find out whether it is independent of habitat variables such as ice condition or water depth.

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Fish Production in Warmwater Streams in Poland and Ontario

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Mahon, R., and E. K. Balon. 1985. Fish production in warmwater streams in Poland and Ontario. Can. J. Fish. Aquat. Sci. 42: 1211–1215.

Density (numbers per hectare), biomass (kilograms per hectare), and annual production (kilograms per hectare per year) of entire stream fish taxocenes were significantly higher at localities in Ontario (n = 11) than in Poland (n = 14). The production/biomass ratio and the mean size of individuals did not differ significantly between the two sets of localities. The average stream size at the localities studied in Poland was significantly smaller than in Ontario. Production and biomass in Poland showed a significant negative association with stream size, whereas in Ontario these relationships were not significant; therefore, the differences in these variables between Poland and Ontario may even be underestimated. Differences in fluvial fish taxocene richness might explain the observed differences in production if the streams in Poland are less saturated than those in Ontario. However, the possibility of more basic differences in productivity at lower trophic levels cannot be ruled out.

La densité (nombre par hectare), la biomasse (kilogrammes par hectare) et la production annuelle (kilogrammes par hectare par an) de toute la faune piscicole en milieu fluvial étaient nettement supérieures à certains endroits de l'Ontario (n = 11) qu'en Pologne (n = 14). Le rapport production/biomasse et la taille moyenne des individus ne variaient pas de façon significative entre les deux groupes. La taille moyenne des cours d'eau étudiés en Pologne était nettement inférieure à celle des cours d'eau de l'Ontario. En Pologne, la production et la biomasse montraient une importante association négative avec la taille du cours d'eau tandis qu'en Ontario, ces relations n'étaient pas significatives. Les différences entre ces variables obtenues dans ces deux milieux peuvent donc être sous-estimées. Les différences au niveau de la richesse de la faune piscicole en milieu fluvial pourraient expliquer les écarts observés pour la production si les cours d'eau polonais sont moins saturés que ceux de l'Ontario. Toutefois, la possibilité de différences plus fondamentales de la productivité aux niveaux trophiques inférieurs ne peut être éliminée.

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Our objective was to examine the productivity of fish assemblages in north temperate warmwater streams. We compared annual production, and related variables, in streams of climatically similar areas (Poland and southern Ontario) on two continents.

Only recently have there been sufficient studies of stream fish production with a consistent methodology for any preliminary attempts at generalization or synthesis. A great deal of the activity in studying fish production in north temperate streams has been focused in two localities: southern Ontario and Poland. Furthermore, in a recent study, Mahon (1984) compared fish taxocene structure in streams of these two climatically similar regions and concluded that there were substantial overall differences in diversity, life history, and morphology. These differences prevailed in spite of the climatic similarity of the regions as regards temperature regime and seasonal pattern of river runoff (Mahon 1984). Land utilization patterns and nutrient loading of the streams, as indicated by conductivity, were similar in the two regions.

As regards the fish taxocenes, longitudinal profiles of species richness indicate a much higher proportion of small-stream specialists in Ontario than in Poland. These fishes are characteristically small, short lived, early maturing, and often exhibit some degree of parental care. In Polish streams, the opposite life history characteristics predominate. In Poland the fishes tend to be more mobile than in Ontario; extensive longitudinal migration within the stream is common. These differences were also reflected in the morphological adaptations of the fishes to stream life. In Ontario, small cryptic benthic forms and fusiform nektonic species predominated, whereas in Poland, large, nektonic, deep bodied forms were far more common.

This divergence in assemblage structure may be in part related to different effects of glaciation on the two continents and in part to differences in richness of ichthyofauna in lowland habitats. The pathways for retreat of fishes into refugia and subsequent recolonization of deglaciated areas were much easier in North America than in Europe. Therefore, European stream habitats could be less saturated than their North American counterparts (i.e. there could be more unutilized resources). Alternatively, lowland habitat specialists in North America may have displaced many other species upstream to become small-stream specialists. Further details and discussion of possible mechanisms are given by Mahon (1984).

In theory, the field study of fish production systems should be

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TABLE 1. Estimates of fish taxocene density, mean biomass, production, and the mean weight of a fish for streams in central Poland and southern Ontario. Mean width of the stream at each locality is given as an indication of stream size.

Stream	Density (no.·ha^{-1})	Mean biomass (kg·ha^{-1})	Annual production (kg·ha^{-1}·yr^{-1})	Mean weight (g)	Mean width (m)	Source
Poland						
Struga R.	39 247	111.2	110.3	4.2	3.0	This study
Lubrzanka R.	17 230	241.0	128.8	21.0	3.5	
Warkocz R.	50 058	307.5	161.4	9.1	2.9	
Bobrza R.	23 698	50.2	83.4	3.2	3.3	
Utrata R.	33 370	310.5	807.2	4.1	1.1	Penczak 1981;
	33 559	142.5	228.0	4.2	2.5	Penczak et al. 1982
	19 595	86.6	329.0	6.7	2.3	
	93 200	45.6	168.7	2.2	2.3	
	6 581	10.8	57.2	2.9	6.1	
	46 055	40.9	147.3	1.6	1.5	
Zalewka R.	6 230	49.8	54.8	8.5	3.5	
	46 327	42.5	76.5	0.8	4.0	
	6 484	38.4	30.7	31.5	5.0	
Wolborka R.	3 714	37.4	35.3	10.4	4.4	Penczak et al. 1982
Mean	30 382	108.2	172.8	7.9	3.2	
Ontario						
Swan Ck.	50 206	124.4	174.5	3.5	4.9	This study
Carroll Ck.	115 125	274.8	280.3	2.6	5.0	
Hopewell Ck.	154 163	228.4	243.5	1.9	6.3	
Irvine Ck.	208 253	149.9	226.4	0.9	10.0	
Ellis Ck.	100 036	376.0	375.4	4.6	4.2	
Upper Carroll Ck.	205 158	278.7	379.1	1.8	3.2	
Mud Ck.	98 000	273.3	409.8	3.5	3.3	Portt 1980
	49 000	61.1	124.4	1.6	4.9	
	38 000	48.2	118.5	1.8	7.2	
North Branch R.	131 000	217.5	500.6	2.0	6.5	
Irvine Ck.	283 537	187.2	297.2	0.8	10.5	Halyk and Balon 1983
Mean	130 227	201.7	284.5	5.1	6.0	

pursued by sampling at regular intervals throughout the year (Chapman 1978), with the aim of accounting for seasonal variability in growth and abundance. However, whenever they have been tested, classical mark–recapture and removal methods for estimating fish abundance have been found to be unreliable, or to require intensive sampling to be reasonably accurate (e.g. Chadwick 1976; Mahon 1980; Pot et al. 1984). In warmwater streams a high proportion of biomass and production is contributed by young (age 0 and 1), small fishes (Neves 1981) for which there are high levels of mortality associated with capture and handling. Hence, a level of sampling intensity that would permit accurate assessment of density and biomass is likely to substantially influence the stream fish assemblage. Consequently, in spite of obvious limitations, we consider that in streams a single, extensive sampling from a representative section is the most appropriate approach to estimating biomass and production. For comparative purposes this approach was used at all the sites discussed in this article.

Materials and Methods

The comparisons are based on 25 estimates of stream fish taxocene production. Twelve estimates, reported here for the first time, were made in the Grand River and Nida River drainage basins in Ontario and Poland, respectively. The remaining 13 estimates, taken from the literature, were for warmwater sites in watersheds adjacent to the Grand and Nida rivers, within 100 km of those presented here. In two of the previous studies the fishes were collected with rotenone (Penczak 1981; Halyk and Balon 1983). In the other two (Portt 1980; Penczak et al. 1982) the removal method of population estimation was employed with a sufficient number of repetitions to be reliable (Mahon 1980).

The Grand and Nida river drainages are similar in many aspects of climate, drainage basin morphology, and land use (Mahon 1981, 1984). Both support warmwater fish taxocenes; i.e. salmonids are either absent or rare. Mahon (1984) presented evidence that these rivers were faunistically typical of rivers in the regions being compared here.

For our study the fishes were collected from sections of stream that were judged typical for their size. At each there was fast flowing water and the substrate was mixed rubble, cobble, gravel, sand, and aquatic vegetation. The fishes were collected using rotenone, which was subsequently neutralised (see Mahon 1980; Mahon and Balon 1980).

For all the localities reported here, and those taken from the literature, production was estimated using Ricker's (1946) method for intervals of 1 yr. Production was estimated for each dominant species at each locality ($P = G\bar{B}$, where G is the instantaneous rate of growth and $\bar{B}$ is the mean biomass). Further details of the methods are given in the cited studies and by Mahon and Balon (1977), Mahon et al. (1979), and Mahon (1981).

Results

The density (numbers per hectare), biomass (kilograms per hectare), and production (kilograms per hectare per year) estimates of this study are presented together with the previously published estimates (Table 1). Average stream width at each locality is used as an index of stream size (Table 1). Nonparametric tests, based on ranks, were considered most appropriate for use with these data. Mann-Whitney U tests (see Conover 1980, p. 216, re assumptions and power of tests; note that we know very little about the nature of the underlying distributions) were used to test the null hypotheses that the two regions do not differ in regard to the mean values of the variables. There were significant differences in density, mean biomass, and production, which were higher in Ontario than in Poland, but none in mean weight of fish or in the production/mean biomass ratio ($P/\overline{B}$ ratio) (Fig. 1; Table 2).

If any of the variables are positively correlated with stream size, the fact that the stream sections were significantly less wide in Poland than in Ontario (Table 2) could invalidate the above comparisons. Spearman's coefficient of rank correlation (Conover 1980, p. 252) was used to determine if production and related variables were associated with mean stream width. For both regions the coefficients for stream width with production, mean biomass, and density are all negative (Table 3). For Poland, two coefficients, mean biomass and production with stream width, are significant (Table 3). These relationships suggest that in streams of similar width in Poland and Ontario the observed differences in production and related variables would be even greater.

Discussion

Fish production of a population or taxocene is the total amount of fish tissue elaborated in a given period, including that which does not survive to the end of the period. It is a useful summary statistic of the performance of a production unit, as it takes into account the major parameters of the unit: biomass, growth, mortality, and recruitment (Neves 1981). Until recently, most fish production studies had been on salmonids in cold-water streams (see reviews by Waters 1977 and Chapman 1978). A review by Neves (1981) cited fewer than 10 studies of warmwater stream fish production. One factor cited by Neves is the relatively small size (i.e. ease of study) of salmonid streams. To this we add that the number of species (i.e. amount of work) contributing to total fish production in warmwater streams is larger; species richness is generally in the order of 12 or 15 species.

Considering the well-known influence of longitudinal physical gradients on the biotic components of fluvial ecosystems (Hynes 1970; Horwitz 1978; Vannote et al. 1980), it is not surprising that some fish production parameters should be significantly associated with stream size. As yet there has been no conceptualization, such as that proposed for invertebrates, of how stream fish assemblage structure and production should relate to stream size (Vannote et al. 1980). The absence of any significant associations of this kind for Ontario streams is probably due to the narrow range of stream sizes sampled in relation to the variability of the parameters being considered. We consider these data inappropriate for further consideration of this aspect of fluvial fish production.

Since the two regions differed significantly in terms of mean biomass but not in $P/\overline{B}$ ratio, it is evident that the difference in

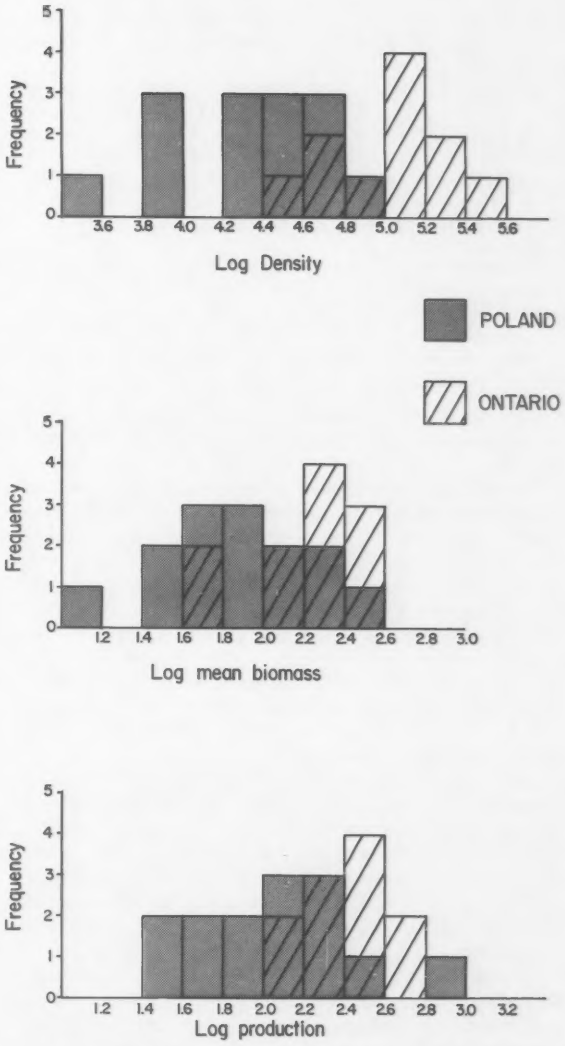

FIG. 1. Comparison of fish taxocene density, mean biomass, and production (log scale) indicates that they are lower in Poland than in Ontario.

TABLE 2. Comparison of production related variables between streams in Poland and Ontario using Mann-Whitney U tests (non-parametric) ($n = 25$).

Variable	Mean rank		U	P
	Poland	Ontario		
Density	8.1	19.3	8.0	0.000
Mean biomass	10.1	16.7	36.0	0.025
Production	9.6	17.3	30.0	0.009
Mean weight	14.8	10.7	52.0	0.183
Production/mean biomass ratio	13.4	12.6	72.0	0.809
Stream width	9.1	18.0	22.0	0.002

TABLE 3. Association between stream width and fish taxocene production variables based on Spearman's coefficient of rank correlation

Variable	Spearman's r (with stream width)	
	Poland ($r_{0.5(2),12} = 0.587$)	Ontario ($r_{0.5(2),9} = 0.700$)
Mean biomass	−0.588[a]	−0.542
Density	−0.586	−0.333
Production	−0.890[a]	−0.324
Mean weight	0.313	−0.360
Production/mean biomass ratio	−0.308	0.510

production is mainly due to a difference in the amount of biomass present rather than the rate of growth ($G = P/\bar{B}$) of that biomass.

Similar $P/\bar{B}$ ratios could be expected in taxocenes with similar size structure, as indicated by mean weight (Banse and Mosher 1980). In theory, a 10-fold difference in mean size would be required to produce a 2-fold difference in $P/\bar{B}$ ratio (Dickie 1972). Although Mahon (1984) observed that the average maximum weight of stream fish species within large river systems of similar size was about eight times greater in Poland than in Ontario, this difference is not reflected in the mean weights at the sites being compared here (Table 2). This apparent discrepancy is most likely due to intraspecific segregation by size of stream fish in Poland, with larger individuals inhabiting larger streams.

The observation that biomass per unit area in small streams is relatively low in Poland is supported by other published data. Penczak et al. (1982) reviewed other estimates of biomass in Polish streams and concluded that they are similar to, or lower than, those observed in the Utrata River and Zalewka Brook (and presented here). Appropriate estimates of stream fish biomass elsewhere in southern Ontario are not available for comparison.

In attempting to explain why streams in Poland should support less fish biomass than streams in Ontario, we are confronted with the usual problem of comparative field studies. There are several, inseparable factors that could have produced the same effect. The lower biomass could be a function of the widespread differences in assemblage structure outlined earlier, and considered in greater detail by Mahon (1984), or due to constraints on fish productivity at lower trophic levels.

In regard to the first question, it is by no means obvious that the lower diversity in streams in Poland should lead to lower density, biomass, and production there. One expectation is that although they were fewer, the species in Poland would have broader niches than those in Ontario, and that this would result in full utilization of all the available resources. The alternative possibility is that there may not be sufficient morphological diversity in the fish taxocene in Poland to make efficient use of the range of available food types. This was suggested to be the case in stream fish taxocenes in Borneo (Watson and Balon 1984).

Our arguments assume that there are similar amounts of available food resources in both regions. However, in spite of physically similar fluvial habitats in both regions, and similar levels of nutrient loading as indicated by conductivity (Mahon 1984), the primary and secondary production systems upon which stream fish production is based may not be generating similar amounts of food. Under apparently similar physical regimes, benthic community structure may differ and influence the availability and suitability of fish prey (e.g. Mills 1975). Unfortunately, there are no comparable estimates of production of stream benthos in Ontario and Poland from which to pursue the question of whether the observed differences in fish production are due to differences in assemblage structure or in resource abundance. It may, however, be significant that the highest recorded estimate of stream benthic production is from a southern Ontario stream (Waters 1977).

Trophic organization of the taxocenes could also, in theory, influence their annual production in several ways. First, a lower average trophic level of fishes should result in a more productive taxocene, assuming similar amounts of resources at the lowest (input) trophic levels. Second, production would be positively correlated to the number of levels of piscivory in the taxocene, since a unit of food energy moving up the food chain within a year would be counted as production at each trophic level. Unfortunately, there is insufficient information to adequately consider the likely contribution of either of these possibilities to the observed differences. It is noteworthy, however, that herbivory is rare among stream fishes of either region. In general, the fishes are opportunistic carnivores. However, ontogenetic shifts in diet are a further complicating factor in considering the trophic structure of fish taxocenes, since individuals of the same species may occupy several adjacent trophic levels depending on their size (Helfman 1978).

Although single sample estimates of stream fish production are relatively crude, they may be the best possible approximation, given the problems of sampling small fish. In fact, this study suggests that accurate estimation of biomass might be more important in assessing overall production than obtaining detailed seasonal estimates of growth and mortality.

This study has brought together all the existing, comparable studies of fluvial fish taxocene production from Poland and Ontario, and has shown significant differences in biomass and production between these two regions. Future directions towards understanding the reasons for these differences are as follows. First, productivity at trophic levels lower than those occupied by the fish should be compared between the two regions. If it is similar, then resource availability and utilization patterns should be compared to determine if the taxocenes in Ontario make fuller use of the available resources than those in Poland.

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NOTES

Phytoplankton Response to Freshwater Runoff: The Diversion of the Eastmain River, James Bay[1]

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Phytoplankton, nutrients, and hydrodynamic conditions were regularly sampled in the estuary of the Eastmain River (Québec) and offshore in James Bay, before and after the diversion of the river for hydroelectric development on 19 July 1980. In the estuary, mean flow decreased by over 90% and the semidiurnal tidal amplitude increased significantly over a 5-d period. The most dramatic event was a major phytoplankton bloom in the river mouth, during a 10-d period of higher water column stability in late August; the cells then remained and bloomed in the thin photic layer. This stresses the role of hydrodynamics (as determined here by the freshwater runoff) in the timing of phytoplankton blooms.

Le phytoplancton, les éléments nutritifs et les conditions hydrodynamiques ont été suivis de façon régulière dans l'estuaire de la rivière Eastmain (Québec) et dans les eaux adjacentes de la baie James, avant et après le détournement de cette rivière pour des fins hydroélectrique, le 19 juillet 1980. En 5 jours, le courant moyen dans l'Estuaire a diminué de plus de 90% et l'amplitude de la marée semi-diurne a augmenté de façon appréciable. L'événement le plus spectaculaire fut une forte poussée de phytoplancton à l'embouchure de la Rivière, fin août 1980, au cours d'une période de 10 jours de stabilité élevée de la colonne d'eau; ceci permit aux cellules d'être retenues et de croître dans la mince couche photique. Ces résultats mettent en lumière le rôle de l'hydrodynamique (sous contrôle ici du débit d'eau douce) quant aux poussées phytoplanctoniques.

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Legendre and Demers (1984) have recently argued that phytoplankton dynamics are controlled by a combination of several hydrodynamic processes, acting on different spatial and/or temporal scales. On the continental shelf and in nearshore environments, the sources of power for vertical mixing of the water column are the winds, the tides, and the freshwater runoff. For example, the timing of the spring phytoplankton bloom has been linked to runoff by Gilmartin (1964) in Indian Arm, a fjord in British Columbia. In addition, Sinclair et al. (1981) have argued that the early vertical stratification provided by freshwater explains why most estuaries bloom earlier than the adjacent water bodies. Their explanation for late blooming estuaries, such as the St. Lawrence, lies in the very high flushing rate attained during the freshet. Sutcliffe (1972, 1973) has correlated the spring runoff in the St. Lawrence with commercial catches of lobster, halibut, haddock, and clams in the Gulf of St. Lawrence, using lags of from 5 to 10 yr. This was explained by the dependence of year-class strength on the timing of the spring bloom relative to the release of larvae in the environment. Changes in freshwater runoff can therefore significantly affect phytoplankton production, and also the whole trophic web including commercially fished species.

Drastic changes in freshwater runoff almost always occur in the springtime, so that it is generally not possible to discriminate their effects on phytoplankton from the other seasonal changes in environmental conditions that occur simultaneously. A unique opportunity to study the response of phytoplankton to a drastic change in runoff was provided by the diversion of the Eastmain River, James Bay (Fig. 1), for hydroelectric develop-

[1]Contribution to the program of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec).

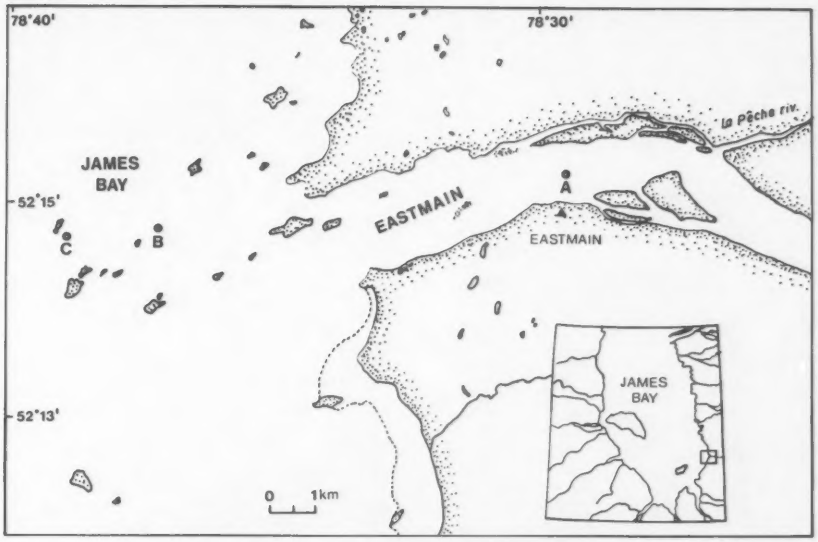

FIG. 1. Study area showing station positions.

ment on 19 July 1980. Prior to 1980, the mean annual discharge was 1200 $m^3 \cdot s^{-1}$, ranging from a monthly mean of 260 $m^3 \cdot s^{-1}$ in March to 2460 $m^3 \cdot s^{-1}$ in June. Mean annual discharge after the diversion was about 80 $m^3 \cdot s^{-1}$, which is a 15-fold reduction. Precutoff oceanographic conditions in the Eastmain have been discussed by Ingram (1982).

Site and Methods

The Eastmain River enters James Bay on its eastern edge (Fig. 1). The river is shallow, with maximum depths of less than 6 m near its mouth. About 5 km offshore, in James Bay (station C, Fig. 1), water depths do not exceed 10 m.

Aanderaa current meters were moored at station A in the estuary (Fig. 1) and station B in James Bay from early June to mid-September 1980 as well as in August and September 1979. Instruments were moored at nominal depths of 2 and 4.5 m, recording speed, direction, temperature, and conductivity at a constant sampling rate of 10 min. Velocity time series were separated into east–west (true) and north–south components. The major axis of the estuary is east–west with the downstream direction westerly.

Relevant biological oceanographic sampling for this study was conducted at stations A and C (Fig. 1). Both stations B and C represent offshore conditions. Their spatial separation is not of great importance, as water mass characteristics differ only slightly between the locations. Water samples were taken at 0 and 5 m at stations A and C on a regular basis in late summer 1979, from late April to September 1980, and from late May to mid-July 1981. Water was collected with a Niskin bottle and filtered on Whatman GF/C. The filters and filtered water samples were frozen for later (1–2 mo) laboratory determination of nutrients (SiO_3, $NO_2 + NO_3$, PO_4) and chlorophyll *a* (in vitro fluorometric method, Strickland and Parsons 1972).

Results and Discussion

The most dramatic effect of the river diversion in 1980 was a major increase in phytoplankton in late August. Prior to diversion, observed surface concentrations of chlorophyll *a* in the Eastmain River estuary (station A) ranged from 1.0 to 1.5 $mg \cdot m^{-3}$. Following the reduction of discharge, surface values increased steadily well above 5 $mg \cdot m^{-3}$ with a maximum of almost 10 $mg \cdot m^{-3}$ on 24 August (Fig. 2). The high chlorophyll *a* values observed between 19 and 30 August 1980 were a unique occurrence in the Eastmain River estuary, since at the same period in 1979, chlorophyll *a* concentrations never exceeded 2.0 $mg \cdot m^{-3}$ (Fig. 2), nor did they in the spring preceding (Fig. 2) or following the diversion (from 24 May to 11 July 1981, not illustrated). Offshore of the river mouth, no significant changes were recorded during the 1980 summer, chlorophyll *a* values ranging at station C between 0.5 and 2.5 with a mean of approximately 1.3 $mg \cdot m^{-3}$.

Changes in chlorophyll *a* concentrations in the estuary (Fig. 2) were paralleled by changes in phytoplankton species. As is generally the case, small microflagellates constantly accounted for about 65% of the enumerated cells, the same being true offshore where they averaged 60%. The bulk of the biomass was, however, made of larger cells. Following the diversion of the river, a diatom species (*Skeletonema costatum*) and a dinoflagellate genus (*Gymnodinium*) that accounted for respectively 45 and 19% of the large cells at station C offshore appeared in the estuary (Fig. 3). This indicated a change from a freshwater to a more marine environment. The bloom at station A was, however, caused by *Cylindrotheca fusiformis* (Fig. 3), a diatom species never encountered at station C, which therefore bloomed locally in the estuary.

Physical and nutrient characteristics of the estuary also changed markedly following the diversion. Circulation characteristics at station A responded quickly to the change in discharge (Fig. 4). Within 5 d of the cutoff the mean flow had decreased by over 90%. Although the tidal signal was irregular immediately after the transition, a significant increase in semidiurnal tidal amplitude was observed within a few days. The establishment of an equilibrium state for salinity did not occur during our observation period, but by mid-August, salinities

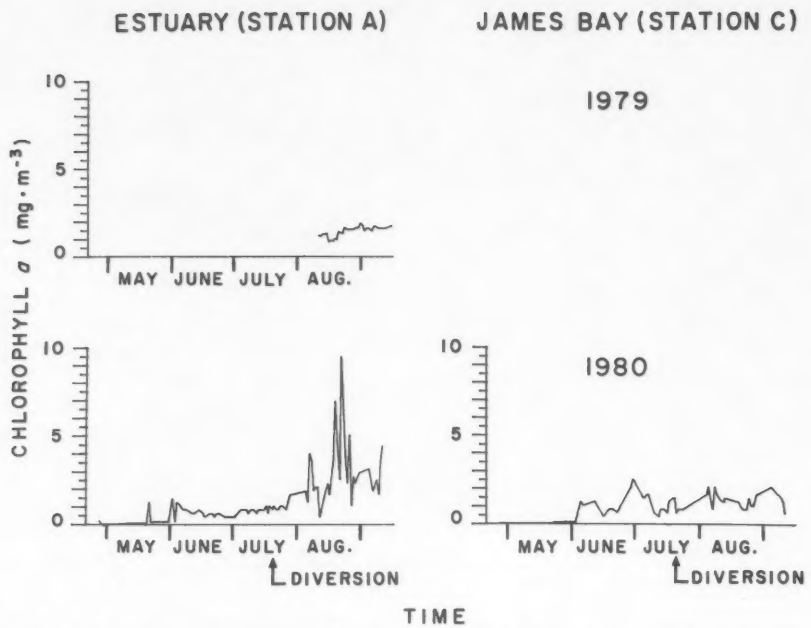

FIG. 2. Surface chlorophyll *a* concentrations at stations A and C from 15 August to 21 September 1979 and from 25 April to 21 September 1980.

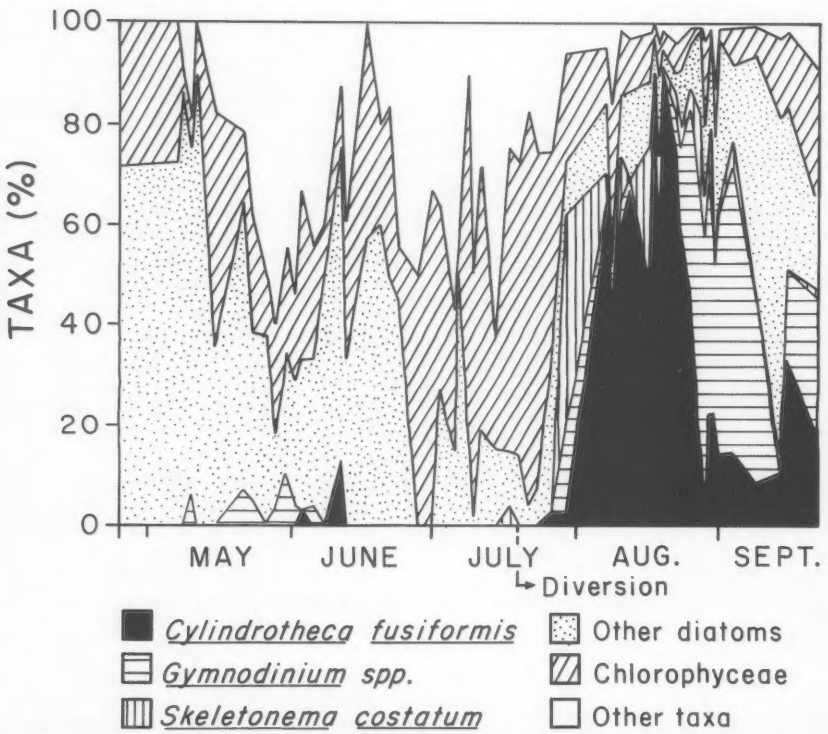

FIG. 3. Taxonomic composition of the phytoplankton (excluding microflagellates) at station A from 25 April to 21 September 1980.

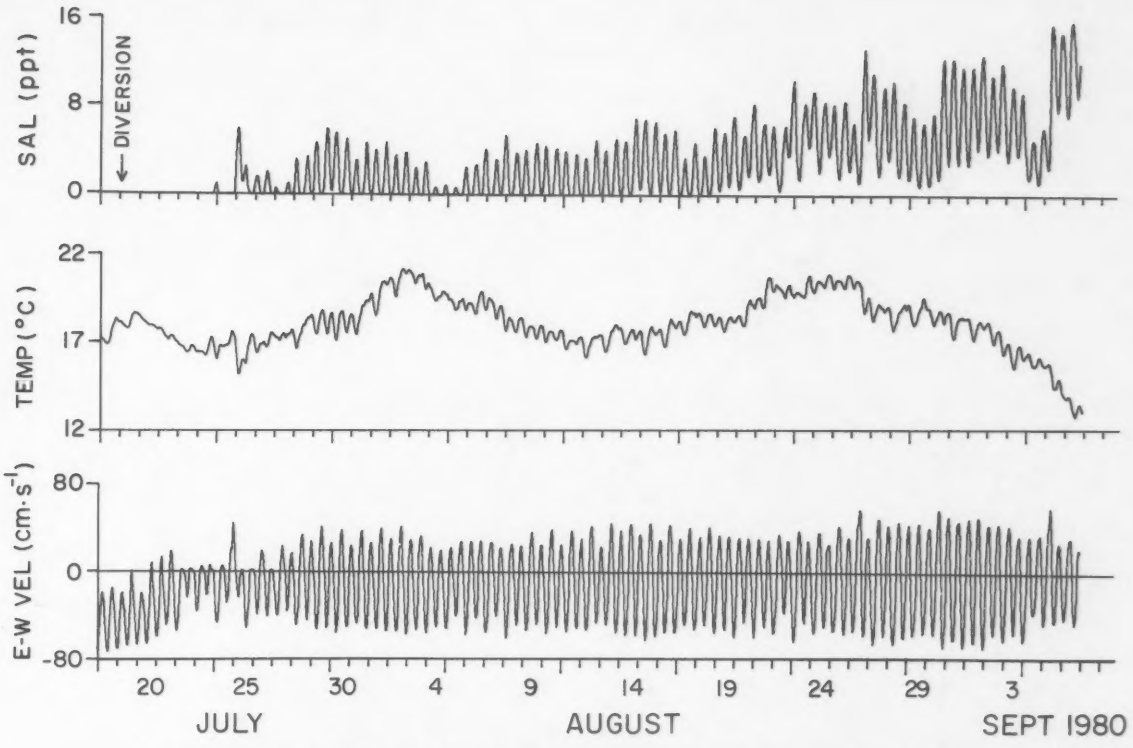

FIG. 4. Time series of salinity, temperature, and east–west current velocity at station A (2 m depth).

above zero were present at all stages of the tide. Water temperature maxima occurred on 2 and 25 August.

At station B (not illustrated), surface salinities increased gradually from about 5 d after the diversion to an equilibrium value of about 17 in late August. The mean current changed between 19 July and 19 August from predominately offshore (west) to a direction paralleling the coast (north). A major contraction of the river plume occurred in consonance with the circulation changes in the Eastmain over a 1-wk period.

Concentrations of the three measured nutrients drastically increased in the estuary after the diversion, to reach much higher levels than under normal flow conditions in 1979 (Fig. 5). The vertical distribution of nutrients showed little variability prior to diversion and a positive increase with depth after diversion. Although no systematic turbidity measurements were taken, the river diversion led in time to the generation of a turbidity maximum zone (B. d'Anglejan, Oceanography, McGill University, pers. comm.) in the estuarine area surrounding station A. Potential postdiversion nutrient sources include advection from James Bay, regeneration within local sediments followed by vertical transport as a result of larger tidal currents, and lateral transport of material resulting from wave erosion on newly exposed river banks as the mean water level decreased by about 0.3 m near station A. The lack of correlation with salinity reflects the nonconservative nature of nutrients and the complexity of their origin. At station A, nitrate availability showed a lead of about 1 wk in comparison with chlorophyll *a* (Fig. 2, 5). Both silicate and phosphate (mainly originating from James Bay) maintained high values throughout the phytoplankton bloom and after, while nitrate (almost absent from James Bay waters at this time of year) decreased during and after the bloom (Fig. 2, 5). This suggests a relationship between the drastic increase in nutrients and the following phytoplankton bloom, as well as between the phytoplankton bloom and the following depletion of nitrate.

To help understand the physical conditions existing in the estuary at the time of the bloom, the gradient Richardson number (*Ri*) was computed throughout the summer of 1980 over the 2.5 m (ΔZ) that vertically separated the two current meters at station A. This number (Turner 1973) compares the stabilizing influence of density stratification to the destabilizing effect of velocity shear. Richardson number is defined here as

$$Ri = \frac{g\Delta\rho\Delta Z}{\rho(\Delta U)^2}$$

where g is the gravitational acceleration, ρ and $\Delta\rho$ are the mean density and the density difference between the two sample depths, and ΔU is the total velocity difference (calculated from both components) between the two depths.

In Fig. 6, *Ri* values are plotted against time for station A. Most of the extremely small values shown are not significant in relation to the instrument precision and are taken to indicate well-mixed conditions. In the absence of salt (before 22 July) at both depths, the density difference resulted from only temperature gradients. Later that summer, from 18 to 25 August, low *Ri* values were generally absent. Higher *Ri* implies a potentially more stable environment, as buoyancy effects dominate the destabilizing effect of vertical shear. The absence of low *Ri* values during the period from 18 to 25 August was the consequence of (1) larger salinities at the lower depth, as this

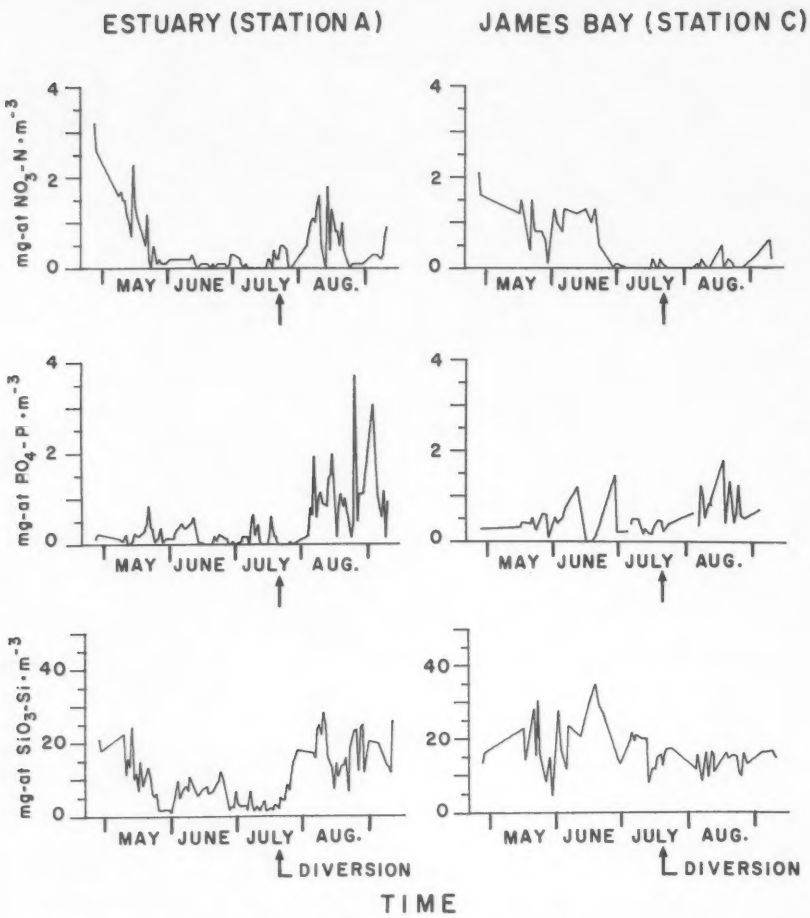

FIG. 5. Surface nutrient concentrations at stations A and C from 25 April to 21 September 1980.

region of the estuary reached a quasi-steady-state equilibrium for salt, which led to a greater vertical density gradient between the two sample depths, (2) a distinct minima in mean flow from 19 to 24 August, as determined from low frequency velocity variations (tidal signals removed), and (3) the presence of smaller tidal currents which reduced the vertical mixing induced by bottom friction (Fig. 6). These changes occurred in the Eastmain estuary only, as the stability of the water column remained unperturbed offshore (station B).

It should be borne in mind that the sampling rate for the biological series differs from that of *Ri*, the former being daily or less in frequency, while *Ri* values were calculated hourly. Some of the variability of the biological series can be explained by the sampling procedures. For example, two of the lowest chlorophyll *a* concentrations observed during the period from 19 to 30 August occurred on 24 and 30 August (Fig. 2), when sampling took place on the flood part of the tide cycle. All other chlorophyll *a* samples were taken at or near full ebb. Keeping this fact in mind, Fig. 2 and 6 show the period of high chlorophyll *a* as the one in which low *Ri* values were generally absent. The increased vertical stability (high *Ri*) reduced vertical motions of phytoplankton in the water column so that the cells remained and bloomed in the thin photic layer (caused by the increased turbidity that followed the diversion). This is confirmed by the fact that chlorophyll *a* concentrations just above the bottom did not change markedly during the period of surface bloom, even though the water column was only 5 m deep. Minimum runoff also favoured the retention of the bloom in the estuary. The observed phytoplankton bloom that occurred upon stabilization of the previously less stable water column is consistent with the production model of Legendre (1981) that was generalized from the "critical depth" model of Riley (1942) and Sverdrup (1953). It is also in agreement with other observations in Hudson Bay, where Legendre et al. (1981) ascribed the under-ice spring bloom to the increased stratification brought about by the low-salinity melting water, and where Legendre et al. (1982) related summer blooms to aperiodic changes in water column stability caused by the combined effects of both winds and fortnightly tides. In the Eastmain River estuary, the increased stability that led to the phytoplankton bloom was caused by a reduction in discharge and tidal currents. The return to low chlorophyll *a* concentration at the end of August can be linked to nutrient depletion (Fig. 5, 6) and also to strong onshore winds, which created less stable conditions in the estuary as shown by the increasing frequency of low *Ri* values from 27 August through the end of the record.

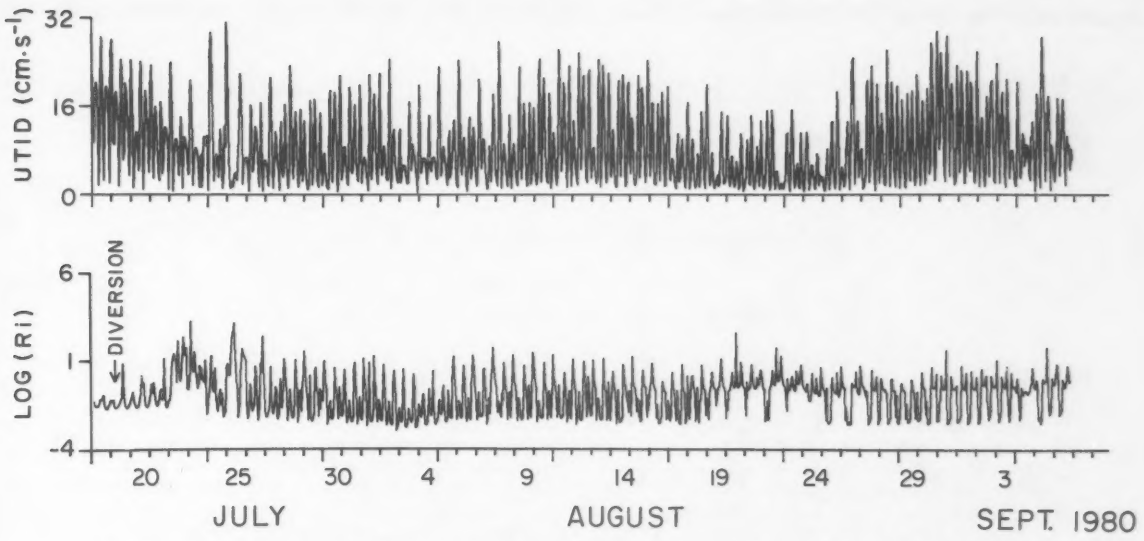

FIG. 6. Tidal current speed at 4.5 m and $\log_{10}$ of Richardson number calculated between 2 and 4.5 m at station A.

In typical shelf conditions (Legendre 1981), nutrient replenishment of the surface mixed layer is dependent on vertical stability conditions, as nutrients are replenished during periods of deep vertical mixing and subsequently used by phytoplankton at the beginning of the following stable period (bloom). In the Eastmain River estuary, these two phenomena occurred independently, since the drastic increase in nutrients that followed the diversion was not caused by increased vertical mixing (see above). However, a phytoplankton bloom developed only when the water column vertically stabilized for several days, which confirms the significant role of hydrodynamics (as determined here by the freshwater runoff) in the timing of phytoplankton blooms.

Acknowledgements

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The Retention of Coho Salmon (*Oncorhynchus kisutch*) Carcasses by Organic Debris in Small Streams

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Cederholm, C. J., and N. P. Peterson. 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. Can. J. Fish. Aquat. Sci. 42: 1222–1225.

Twenty marked coho salmon (*Oncorhynchus kisutch*) carcasses were placed in each of nine small streams on the Olympic Peninsula of Washington during the fall–winter spawning period. Distribution of the carcasses in 500 m of stream below each release site was followed for 4 wk. One week after placement, 78 of the 180 carcasses were found in the nine study reaches; 80% were found in the first 200 m downstream of the release sites. A general positive trend was observed between the number of carcasses retained and the amount of debris in the stream channel ($r = 0.61$). Terrestrial animals rapidly consumed carcasses during the experiment, and removed many of them to the riparian zone.

Cent quatre-vingt cadavres marqués de saumon coho (*Oncorhynchus kisutch*) ont été répartis également dans neuf petits cours d'eau de la péninsule Olympique (Washington) pendant la période de fraie en automne et en hiver. La distribution des cadavres sur 500 m en aval de chaque lieu de lâcher a été suivie pendant 4 sem. Une semaine après leur lâcher, 78 des 180 cadavres ont été trouvés dans les neuf secteurs étudiés; 80 % ont été trouvés dans les 200 premiers mètres en aval des lieux de lâcher. On a observé une tendance positive générale entre le nombre de cadavres retenus et la quantité de débris présents dans le chenal ($r = 0{,}61$). Les animaux terrestres ont rapidement mangé les cadavres au cours de l'expérience et ont en amené un bon nombre dans la zone ripicole.

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Salmon carcasses may be an important source of nutrients (especially phosphorus) in oligotrophic lakes (Juday et al. 1932; Donaldson 1967; Foerster 1968). The seasonal consumption of salmon carcasses by wildlife species such as bald eagles (Glock et al. 1980; Hunt and Johnson 1981), black bear (Frame 1974), and other animals (Meehan 1974) has been documented. However, with the exception of one study (Richey et al. 1975) the beneficial effects of this type of organic subsidy on salmonid populations in lotic environments remains poorly understood. In their work with kokanee salmon (*Oncorhynchus nerka*) in tributaries of Lake Tahoe, Richey et al. (1975) inferred that additional phosphorus and nitrate available due to carcass decomposition was responsible for subsidizing the ecology of Taylor Creek. Under historical conditions and prior to the development of extensive commercial and sport fisheries, the direct and indirect nutrients supplied from salmon carcasses may have contributed significantly to productive riparian and aquatic ecosystems (Houston and Contor 1984).

In the steep coastal drainages of the Pacific Northwest, high rainfall and runoff rates leach chemical nutrients from the land and vegetation (Tarrant and Trappe 1971; Larson 1979; Vitousek et al. 1979). It follows that salmon may return nutrients and needed trace elements to the aquatic and terrestrial environments (Brown 1982).

Abundant accumulations of organic debris in natural stream channels are an essential component of salmonid spawning and rearing habitats (Swanson and Lienkaemper 1978; Bryant 1983), and may play an additional role of retaining carcasses in the lotic environment for eventual biological processing (Sedell et al. 1983). However, extensive stream clearance (Sedell and Luchessa 1981; Bryant 1983), channelization (Cederholm 1972), salmon barrier removal (Bryant 1983), past improvement work (Kramer 1953), and high utilization forestry practices (Grette 1985; Toews and Moore 1982; Bryant 1983) have resulted in either direct removal of existing organic debris from stream channels or the loss of future sources of debris from the riparian zone.

We speculate that a reduction of organic debris in streams can result in fewer salmon carcasses being retained for in situ biological processing. The purpose of this experiment was to test the hypothesis that streams having higher amounts of organic debris will retain relatively more salmon carcasses.

Methods

For logistic convenience and similarity of climate, we chose nine study streams having a range of debris abundance, in close proximity to Forks, Washington (Fig. 1), using information supplied by Grette (1985). The streams are all within 40 km of each other. The mean annual rainfall in the Forks vicinity is 300 cm, and twice during this experiment rain storms caused the streamflow to reach near bankfull discharge. Basin areas of the

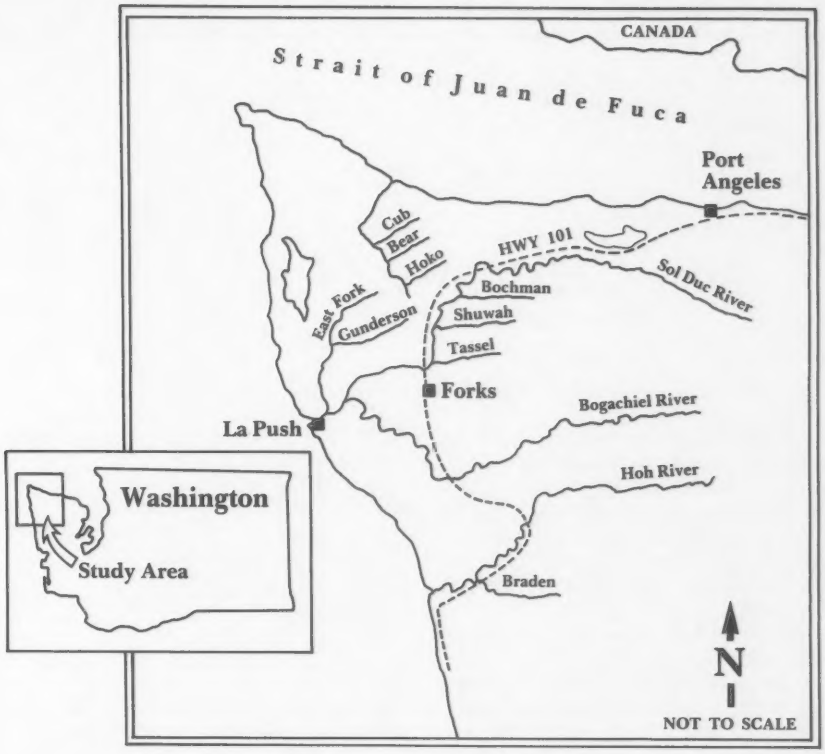

FIG. 1. Location of study area.

experimental streams ranged from 5.2 to 9.8 km^2, averaging 7.7 km^2; channel gradients ranged from 1.0 to 2.0%, averaging 1.4%.

We randomly selected a 500-m-long study reach in each of the nine streams. Within these study reaches, the number of logs (large organic debris, LOD) greater than 10 cm in diameter, and at least 3 m long that were either in the water or within up to 1 vertical m of the water surface, were counted. Small organic debris (SOD) was also quantified, and was defined as anything smaller than the LOD down to a minimum of 2.5 cm in diameter and 0.5 m long. Mean width of the ordinary high water channel was also measured (Table 1). All the streams had been logged approximately 30 yr ago.

On November 23, 1983, we introduced 20 (1:1 sex ratio) coho salmon (*Oncorhynchus kisutch*) carcasses into each of the nine study streams. The 180 carcasses were supplied by the Washington Department of Fisheries (WDF) Sol Duc River Salmon Hatchery. Male carcasses were intact, but the females had been cut open during artificial spawning. All the carcasses were tagged through the body wall with an orange plastic interlocking connector.

Carcasses were placed in the thalweg of the stream, within 10 m of the upstream end of each study reach. During four subsequent weekly surveys the physical condition, stream location, and retention mechanism were recorded for all observed carcasses. None of the carcasses were removed by the survey team and all observations were restricted to the 500-m study reaches. When a salmon carcass was discovered, we noted the degree of utilization by scavengers.

In addition, one survey was made of a 10-m-wide band of streambank on both sides of each study section to look for tags and carcasses outside the high water marks of the streams, as another indication of scavenger activity.

Results

Seventy-eight (43%) of the 180 released carcasses were found 1 wk after they were placed in the streams. On this initial survey the number of salmon carcasses accounted for in the individual stream sections ranged from 3 to 14 (Table 1). The higher numbers of carcasses accounted for were found in the streams with higher debris abundance. Half of the discovered carcasses were male and half were female. Fifty-five carcasses had tangled in organic debris, 12 were either laying on or buried in the substrate, 11 had hung up on live alder roots, and 15 of these carcasses had been partially or completely consumed by scavengers. In the case of scavenged carcasses, often only the plastic tag and some pieces of flesh and bone remained. Of the 55 carcasses tangled in debris, only 18 (33%) rested directly on LOD. The remaining 36 (67%) rested directly on a matrix of SOD, which in many cases was supported by a "foundation" of LOD. The debris that caught carcasses was often clumped into small jams.

Combined data from all nine streams showed that 54% of the carcasses were retained in the first 100 m and 26, 10, 8, and 3% in the next four downstream 100-m reaches, respectively. The furthest downstream discovery of a marked carcass was 418 m.

The number of carcasses found in each of the nine study

TABLE 1. Some characteristics of the 500-m study sections.

Tributary	Stream gradient (%)	Basin area (km^2)	Mean bankful width (m)	Bankful channel wetted area (m^2)	LOD		SOD		First week survey carcass count
					Total	No./100 m^2	Total	No./100 m^2	
Cub	2.0	5.2	9.2	4604	140	3.04	531	11.53	5
Bear	1.4	9.8	15.4	7683	98	1.28	389	5.06	3
East Fork	1.1	6.5	10.0	5000	211	4.22	326	6.52	9
Hoko	1.0	8.8	12.2	6098	98	1.61	209	3.43	6
Shuwah	1.5	9.1	12.6	6326	184	2.91	549	8.68	14
Bockman	1.2	7.5	9.9	4985	156	3.13	441	8.85	13
Gunderson	1.5	8.0	8.6	4299	185	4.30	494	11.49	10
Tassell	1.1	7.2	7.7	3872	138	3.56	362	9.35	14
Braden	1.4	8.5	10.1	5046	109	2.16	435	8.62	4

reaches (Table 1) was regressed on the number of LOD and SOD pieces (Table 1). In addition, the relative expression of the debris abundance for both LOD and SOD was substituted as the independent variable in linear regression analysis. The correlation coefficient (r) was 0.611 for LOD pieces, and 0.605 for LOD pieces/100 m^2 bankfull wetted area (Fig. 2). Regression analysis showed no apparent relationships between SOD and carcass retention (Table 2).

Based on tracks, it appeared that racoons were the principal mammalian scavenger. After the first week, only 15 carcasses (19% of the total discovered) showed signs of being scavenged; after the second week, 60 (77%) showed signs of usage; and by the completion of the experiment, 73 (94%) of the discovered carcasses had been either partially or fully consumed by animals. The odor around some log jams and the partial burial in the streambed of some carcasses suggested that there were probably some carcasses not visible to us. After the fourth week, three carcasses (all covered with fungus) remained unscavenged.

On January 3, 10 d after the experiment was complete, 43 tags and carcass remains were found within the 10-m streambank zones, indicating that many carcasses had been consumed outside the high water mark in the riparian corridor. Some of these tags may have already been counted with the original 78 carcasses.

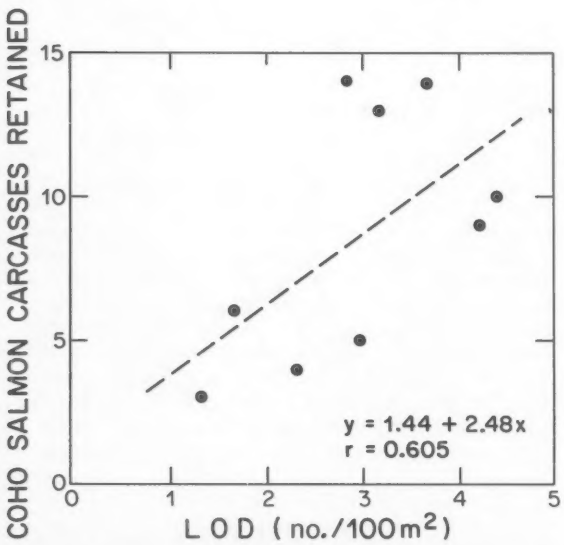

FIG. 2. Relationship between large organic debris (LOD) and coho salmon carcass retention in nine small streams.

TABLE 2. Relationships between organic debris and coho salmon carcass retention.

	y-intercept of line	Slope of line	(r)
LOD (total)	−0.89	0.06	0.611
LOD (no./100 m^2)	1.44	2.48	0.605
SOD (total)	5.09	0.01	0.213
SOD (no./100 m^2)	4.32	0.53	0.333

Discussion

An important first step in answering the larger question of ultimate carcass nutrient disposition is to determine the immediate fate of the carcasses themselves. This first step is critical to establishing the pathways whereby nutrients may return to the fish. One commonly held belief is that salmon carcasses are quickly flushed from streams after spawning, especially during the winter spawning period of coastal fall coho and chinook (*Oncorhynchus tshawytscha*). This line of reasoning may lead to the conclusion that anadromous fish carcasses do not appreciably contribute to stream productivity, and therefore could not indirectly support the production of succeeding generations of fish. In contrast, this experiment indicates that in the tributary streams that typically support the bulk of freshwater coho production from large river systems, carcasses are not quickly lost to downstream areas. Carcasses are tangled in accumulations of organic debris or entrained in the streambed near where they spawn. Many others are removed to the riparian zone by scavengers and consumed there.

The organic debris loading of natural unlogged streams is considerably greater than was found in our experimental second-growth streams. Grette (1985) found an average of 299 pieces of LOD/500 m in similar nearby unlogged streams, which is over 100% greater than we found in our streams ($\bar{X}$ = 147 pieces/500 m). This indicates that many more carcasses would have been retained by debris if our experiment had been conducted in unlogged streams.

Our findings suggest yet another function of LOD in streams.

The variety of beneficial functions performed by LOD in support of fish and wildlife populations will be best perpetuated by protecting naturally occurring accumulations in the stream channel during logging, and by preserving some standing timber in the riparian zone for future recruitment.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment

I was intrigued to read the recent "Perspective" by Michael Gilbertson entitled "Need for development of epidemiology for chemically induced diseases in fish in Canada" (Can. J. Fish. Aquat. Sci. 41: 1534–1540). I'm sure Dr. Gilbertson intended it to stimulate discussion, but I think he oversimplified many issues.

Dr. Gilbertson made two basic points: first, that the current science of aquatic toxicology is inadequate to support legal and management actions to control pollution and toxic chemicals; and second, the cause was a preoccupation of aquatic toxicologists with laboratory testing; they should shift their attention to an epidemiological approach (epizootiology — the study of diseases in wild animals). He also made a number of statements that are controversial due to errors in interpretation or fact.

Science and the law

Dr. Gilbertson contended that actions against polluters under Section 33 of the *Fisheries Act* depend too much on "expert evidence" and that formal proof of damage to fisheries is needed to obtain convictions in today's economic climate. However, the legal actions in British Columbia and Alberta that he cited show just the opposite. In British Columbia, the Department of Fisheries and Oceans (DFO) has gained many convictions under Section 33 and seems to be more successful each year. In Alberta, the cases cited show a reversal of precedents since 1980. Previously, it was necessary to demonstrate real damage to fisheries; now, all that is required is the testimony of an expert witness that a substance deposited in waters inhabited by fish was deleterious.

It is also unrealistic to demand that changes to effluent regulations be justified only by proof of real damage to fisheries. Damage can only be *estimated*, since natural variability in fish mortality, reproduction, growth, and population size (the criteria most easily understood and accepted) preclude absolute proof (Vaughan et al. 1984). In laboratory tests, variability can be controlled and the threshold of toxicity measured. We assume, however, that there is an increasing risk of harm to fisheries at exposure levels above the threshold of toxicity. While the nature and extent of this harm is unpredictable, we should not regard a low level of toxicity as trivial simply because it is hard to prove in the field: "The cumulative effects of multiple stresses on fish populations may cause the collapse of a population, even though the effects of a single stress may be insignificant" (Vaughan et al. 1984).

Effluent regulations must therefore balance the risks to fisheries against the social and economic costs of pollution control; hence, decisions on regulations become political. Dr. Gilbertson was correct to say the economy affects regulations but incorrect in identifying the problem as aquatic toxicology.

A similar view can be taken of the *Environmental Contaminants Act*. Dr. Gilbertson stated that it "requires the Federal Government to gather data on likely benefits of the proposed regulation (of toxic chemicals)". He interpreted this to mean "that we need a measure of the actual damage and of the likely increases in fish production that will accrue from implementation of the regulations." From a fisheries standpoint, this idea is wrong. DFO should not justify a regulation on damage that is extremely difficult to prove and of uncertain economic value. Rather, it should recommend actions that will conserve existing fisheries by minimizing risks; regulations and expenditures on toxicology are a form of insurance against future losses as well as a means of correcting current problems. DFO's responsibilities go beyond regulating chemicals and effluents to include the conservation and enhancement of fisheries and the ecosystem that supports those fisheries. Should DFO have to prove under the *Fisheries Act* that fisheries were damaged, or should polluters have to show that damage was not done?

I also do not think it practical or desirable to judge science by rules of legal evidence. Science advances by hypothesis, inference, and inspiration. If scientists had to prove their case in court to justify support, we would regard Mendel as an eccentric botanist and would not have the miracles of molecular genetics. Dr. Gilbertson cited the case of acid rain: in the United States, research has been substituted for controls because the wealth of data on acid effects has not proved conclusively that acid exterminated fish in Adirondack Lakes. From this example, Dr. Gilbertson advocated fundamental changes in the approach of science and scientists to relating cause and effect, because "politics ... has changed the rules of evidence ...". Here again, he has changed a political problem to a scientific one. If there is no political will to solve the acid rain problem, no amount of science will solve it. The real need is for stronger links between science and politics, since this problem will be resolved in the political forum.

There is also the time element. Do we wait another 20–30 yr for "new science" to show that more fish populations have succumbed to acid before we implement controls? At what point do we say that the risks and costs of losing fisheries outweigh the risks and costs of over-regulation? When do we insist on "proof" and when do we take a chance on scientific inference and opinion? By analogy, since we already know that lead is highly toxic, do we wait for symptoms of lead toxicity in children before we limit emissions?

An example is the "case history" of DDT. After many years of study, the "formal demonstrations" of cause and effect urged by Dr. Gilbertson were not possible and DDT use was banned by inference and scientific judgement. Only in the case of chemical effects on mink reproduction was a "formal demonstration" achieved; the mink were in a "ranch" and laboratory experiments easily related cause and effect by duplicating exposure and holding stresses. Given the variety of stresses affecting most aquatic ecosystems, it is unlikely that conclusive demonstrations will ever be possible no matter how long we study. Should we not learn from these examples and act quickly rather than recommending more research?

Field versus laboratory investigations

Dr. Gilbertson was quite critical of laboratory toxicology:

> By not starting with a disease, aquatic toxicologists have not focussed their work on critical compounds and pathways and thus have been unable to contribute very much except to say which compounds are very toxic and should not be put into the aquatic environment at more than a certain concentration.

This incredible statement ignores the major role of aquatic toxicology in pollution control. Aquatic toxicology arose from a reluctance to implement pollution control until chemicals or effluents could be shown to be harmful to aquatic biota. From laboratory research on cause and effect, specific water quality objectives were developed to limit pollution discharges because they provided (Hodson 1980) (1) a goal to be achieved, (2) a scale against which to measure current water quality, (3) design criteria for pollution control engineering, (4) perspective on current and proposed water use, and (5) a scientific basis for standards, guidelines, and regulations. The utility of objectives is shown by their inclusion as a major part of pollution control programs in the United States, under the *Canada–U.S. Agreement on Great Lakes Water Quality* (1978), and increasingly, in water management across Canada. As a proactive approach to limiting toxic chemicals, aquatic toxicology to develop objectives is a highly appropriate part of fisheries protection by DFO.

The major problem with objectives is that they cannot prevent environmental effects due to untested chemicals or unexpected interactions. Hence, I completely agree with Dr. Gilbertson that we need epizootiology. I cannot agree, however, that it should be the principle approach as he implied; we need both. Currently, epizootiology can show us diseases in fish populations and relate them to pollution, but it cannot clearly establish cause and effect. An excellent example is a 4-yr multidisciplinary study of fish diseases in Puget Sound (Malins et al. 1984). While prevalence of fish diseases increased with proximity to pollution, the chemical(s) responsible could not be identified. The authors concluded:

> Using this multidisciplinary approach, we have pushed the field assessments to nearly their productive limits, yet still many uncertainties remain. It is apparent that carefully controlled laboratory studies provide the best hope for further elucidating the causes of the observed lesions.

If we rely primarily on epizootiology, our fisheries will be the first indicators of problems. By the time we have characterized an effect, shown that it is related to chemical pollution rather than to climate, overfishing, disease, etc., and convinced industry to clean up, pollution control may be too late to protect fisheries. This was the case with DDT and Atlantic salmon. The more stressors affecting fish, the longer it will take to evaluate the role of toxic chemicals. Therefore, we must detect chemical effects on real fish populations at the earliest possible moment (Rapport 1984).

Since chemical toxicity starts with a molecular interaction, molecular events provide the earliest sign of the presence and effect of chemicals. Dr. Gilbertson has badly misinterpreted the efforts by aquatic toxicologists to use biochemical responses for just this purpose. He stated:

> I believe we have excessively concentrated our efforts on development of oversophisticated biochemical techniques that are not specifically diagnostic of particular chemically induced diseases, i.e. they are not pathognomonic techniques.

Dr. Gilbertson has obviously missed the work of Dr. J. Klaverkamp, DFO, Winnipeg. From field observations by Van Loon and Beamish (1977), he developed a field and laboratory study to show that fish in metal-contaminated lakes were metal resistant, and that this resistance was due to induction of biochemical detoxification (Klaverkamp et al. 1984). Dr. J. Payne, DFO, St. John's, used the induction of liver enzymes in marine fish to demonstrate in the North Atlantic that the toxic effects of oil drilling were limited to very small areas around the rigs (Payne 1984). The approach recommended by Dr. Gilbertson would require years to arrive at the same conclusion. I have developed an enzymatic test for lead exposure in fish that is sensitive, specific, and predictive of toxic effects, an example of a pathognomonic technique (Hodson et al. 1984). In fact, my laboratory work on enzyme inhibition prompted the field studies (quoted by Dr. Gilbertson) that associated scoliosis in pike with lead contamination. I cannot agree that field observations must precede laboratory bioassays for relevant toxicology, nor should aquatic toxicologists ignore laboratory studies. A very good example is Dr. Gilbertson's own hypothesis concerning the possible occurrence of "chick edema" disease in Great Lakes fish — he clearly cited a laboratory bioassay by Helder (1980).

What is notable about the examples above (and there are many others) is that those developing "oversophisticated biochemical techniques" have also been involved in the study of real problems. Rather than criticizing biochemical studies, we should foster them to make epizootiology a more cost-effective and rapid way of protecting fish populations.

Dr. Gilbertson implied that most fish toxicology is directed to predicting the fate and effects of new chemicals, an effort he felt was misguided given the relatively small number of such chemicals. Again, he is only partly right. A major effort is directed to predictions, but through the understanding of existing problems, I do not know of any laboratories in Canada currently devoted to new chemicals. As a relatively new science, aquatic toxicology has very little *general* understanding of fate and effect, and specific data takes many years to accumulate for each chemical. As Dr. Gilbertson pointed out, adequate testing of every chemical is unrealistic, but the answer is not lengthy field studies. A predictive capability is essential, whether we are concerned with chemicals new or old, and the current efforts in this area are highly justified.

Dr. Gilbertson must be commended for his systematic approach to experimental design for field studies; coupled with Green's (1979) statistical advice they provide an excellent framework for designing studies of chemical effects on aquatic ecosystems. However, Koch's postulates do not always apply to studies of chemicals as well as to studies of bacteria. Chemicals are often more ephemeral and difficult to measure than bacteria, and their metabolism may give us effects without obvious cause. We also cannot confirm a suspected cause by polluting unaffected ecosystems and we can rarely wait for chronic or latent toxicity (e.g. the development of tumours). Here again, we need the savings provided by a biochemical approach to toxicology. The application of Koch's criteria will be very limited and "formal demonstration" of cause and effect less possible.

I find Dr. Gilbertson's prescription to toxicologists to be "naturalists" very unrealistic. If we are to be credible as scientists, we must prepare suitable experimental designs based on real problems, questions, and hypotheses. Environmental surveys without well-defined hypotheses are very wasteful (Green 1979); while we certainly must look for unexpected responses, it is essential to focus sample collection and analyses.

Is this discussion academic, however? According to Dr. Gilbertson:

> The critical place to look, of course, is in the Great Lakes where, particularly 10 yr ago, there were not only the highest levels of individual pollutants such as PCB and dioxin but also the greatest diversity of persistant and biologically active compounds. But it is rather late to start looking for effects, even in Great Lakes biota, because the levels are now very low compared with the levels in the past. If they were not overt then, it is unlikely that anything can be seen now.

Is he saying that even epizootiology is futile? Apparently, he has overlooked the *rising* levels of contaminants and prevalence of tumours in Great Lakes biota (IJC 1983), severe chemical contamination elsewhere in Canada (e.g. Sydney Harbour, Nova Scotia), and new analytical techniques that reveal problems unknown 10 yr ago. I do not believe we know the true extent of environmental contamination near most industrial areas of Canada. Now, more than ever, we need *all* the tools of toxicology, used in concert, to identify the threats to Canada's fisheries.

We should applaud Dr. Gilbertson for provoking thought and discussion, but his views should not be accepted as the last word on the subject — Peter V. Hodson, *Environmental Toxicology, Great Lakes Fisheries Research Branch, Department of Fisheries and Oceans, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6.* (J8102a)

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Reply

Peter Hodson's letter, I think, underlines my conclusions that aquatic toxicology "is still experiencing a crisis of epistemology" and that "there is a priority requirement for the development of a symbiotic relationship between laboratory experimentalists and field observers." Perhaps because of this, Dr. Hodson and I are not as far apart as his letter might imply.

One of the central problems with aquatic toxicology is where to start. I have contended that aquatic toxicology should start with "observations of field populations to see whether any anomalies are occurring." After these initial signals or "early warnings" have been detected we can then undertake surveys to find out the extent of the incidence of the anomaly and start testing some hypotheses about causation. After we have a plausible explanation from laboratory experimentation we can go back to the field to see whether the laboratory findings still hold and whether there is sufficient evidence to bring about some regulatory control action. Recently, during the past decade, aquatic toxicology research has started with a chemical and laboratory experimentation and finally moved into the field.

Dr. Hodson stated that I implied that epizootiology "should be the principal approach" and that he could not agree with this but felt that both epizootiology and laboratory toxicology are needed. There should be no need to disagree about this because I have already stated I want the "symbiotic relationship." I am concerned, however, about how little epidemiology is being undertaken and about the sequence of the work. The four examples that Dr. Hodson cited would seem to underscore my point. The Puget Sound studies (Malins et al. 1984), the metal resistance studies (Klaverkamp et al. 1984), perhaps the liver enzyme studies (Payne 1984), and certainly the hypothesis (Gilbertson 1984) of the "chick edema" analog (Helder 1980) all started in the field. The excellent Puget Sound studies are an American example of what I would like to see developed in Canada. I omitted the metal resistance and liver enzyme studies from the case histories because I did not consider them to be diseases but "physiological compensatory mechanisms." True, if the mechanism becomes saturated a disease may ensue but the detoxification mechanism is not the disease. I have already acknowledged that monitoring these biochemical mechanisms may be a useful means of detecting "early warning" signals that a chemical is present and causing subclinical "effects." These four examples are, however, rather unusual in that they started from field observations of biological anomalies. In contrast, most of current aquatic toxicology starts with the detection of yet another chemical in an environmental sample.

This leads to the next problem, which I see as the definition of the objective or purpose of aquatic toxicology. Most aquatic toxicologists to whom I have talked justify their work as being important for the *prevention* of problems through understanding the principles of the mode of action of toxicants so as to *predict* the likely effects of chemicals. This is a laudable raison d'être and essential for testing new chemicals and investigating specific problems posed by existing chemicals. But if one is located on top of a seriously polluted water body, prevention and prediction have to take a back seat and the prime objective becomes documentation of the existing state of affairs so that a persuasive scientific and legal case can be made to stop the polluters. If you are located at the scene of a chemically induced crisis, such as Lake Ontario during the past 20 yr, how do you

put together a convincing case that will persuade a company, such as Occidental Petroleum Corporation (that took over Hooker Chemicals and Plastics Corporation), that they have to spend hundreds of millions of dollars to clean up their dump sites? In my opinion, the best approach is to get out onto Lake Ontario to see if Occidental has caused any damage to the fish and if there would be any benefits from cleaning up the chemical landfills. Canadian scientists, administrators, and politicians are having to deal with U.S. industrialists that are skeptical of the allegations of damage. We are also having to deal with a foreign government that does not want any outside encroachment on its sovereignty.

Dr. Hodson stated that I ignored the major role of aquatic toxicology in developing water quality objectives for pollution control and cited their inclusion in the 1978 *Canada–U.S. Agreement on Great Lakes Water Quality* as an example of their utility and "as a proactive approach to limiting toxic chemicals." I wish such had been the case. In reality, their inclusion was a reactive approach to try to start limiting the discharge of persistent toxic substances that were causing havoc with the fisheries and with wildlife and, if the Lake Michigan human epidemiology data (Fein et al. 1984) are to be believed, with human reproduction. Unfortunately, the numbers have enabled officials to state that the results of chemical analyses show that most of the time the concentrations of persistent toxic chemicals, for instance in the Niagara River, meet the objectives and thus the discharges are not out of compliance. I have argued elsewhere (M. Gilbertson, manuscript in preparation) that the water quality objectives for organochlorine chemicals contained in Annex 1 of the Agreement should be deleted and that the philosophy of zero discharge and virtual elimination contained in Annex 12 should take precedence for discharges of these "persistent toxic substances."

Dr. Hodson challenged my interpretation of the Cabinet Directive on health, safety, and fairness regulations. He said that "DFO should not justify a regulation on damage that is extremely difficult to prove and of uncertain economic value." As part of my job, I negotiate with industry concerning new or revised regulations under the *Fisheries Act*. Some of these are to require industry to upgrade their treatment facilities that were built, at no small expense, within the past 10 yr. If I do not know what the improvement to the fishery has been from these investments nor how much it will improve with the next investment, I am in an unenviable negotiating position. In all sincerity, I invite Dr. Hodson to help me in the future negotiations with industry. The Environmental Protection Service is in the process of preparing a socioeconomic impact assessment for the possible proposed revisions to the effluent regulations for the pulp and paper industry. The task has, however, proved extremely difficult because of the lack of data on value of the fisheries at risk, on the scale of the damage, or on the likely benefits. Is Dr. Hodson suggesting that the SEIA is not needed and that its preparation is due only to a wrong interpretation of the Cabinet Directive?

Dr. Hodson agreed with me that decisions on regulations are affected by the economy and that they become political. He disagreed that aquatic toxicologists need to "formally demonstrate" damage to fisheries or benefits of cleanup and that the "rules of evidence" have changed. He then cited the example of acid rain as an example of a problem which is not soluble by science because there is no political will. How good is the evidence concerning the extent of damage caused by acid rain? J. R. M. Kelso and C. K. Minns (Department of Fisheries and Oceans, Ontario Region, pers. comm.) have synthesized the data on various parameters of Canadian fish populations to see whether they could detect correlations with pH and alkalinity. This is much the most comprehensive synthesis that has been undertaken, but apart from indicating a lower diversity with increasing acidity there were no clear-cut associations with the presence or absence of particular fish species nor with benthos, zooplankton, or phytoplankton. We know several areas where there have been unequivocal effects of acid rain, but there is still a large area of uncertainty about the rate at which lakes are likely to acidify. These uncertainties are amenable to science and are a prerequisite to successful politics.

Dr. Hodson has, quite rightly, posed the question "when do we insist on "proof" and when do we take a chance on scientific inference and opinion?" My problem is that I have not found too many industrialists or foreign politicians who want me to gamble with their money. They want the evidence that supports our allegations of damage so that they can go back to their boards of directors or their constituencies and raise the megabucks for cleanup. I wish we could "act quickly rather than recommend more research." I wish we did not have to "wait for symptoms ... before we limit emissions." My argument is that epidemiology is one of the indispensible pieces of evidence needed in trying to negotiate regulations and cleanup and to prevent further damage. I argue that epidemiology has been sorely neglected in Canada during the past decade and a half, though apparently not during the previous decade, and it is time to restore it as an important tool in aquatic toxicology. How much epidemiology, compared with laboratory toxicology and chemical analysis, is appropriate is a matter of managerial fine tuning. The amounts allocated during the past decade, I argue, have been insufficient to find initial signals of damage that was actually occurring and to help compile comprehensive scientific cases for regulatory decision-making.

I am not advocating that we should give up laboratory toxicology and do only epidemiology, nor that we should manage chemicals solely by looking for their effects in the field after they have been brought into commerce. This would be chemical suicide. We need preliminary test data for screening chemicals new to commerce. We need to make detailed assessments of those that look suspicious to prevent their entry into commerce if they are bad actors. We need a science of aquatic toxicology to understand, even at the molecular level, how organisms respond to chemicals. However, when the system breaks down, as it has on the Great Lakes during the past quarter century, and we are faced with a massive chemical crisis, the priorities and approaches have to change. One of these approaches that has, in my opinion, been neglected both for humans as well as aquatic organisms is epidemiology and this should be rectified as quickly as possible.

I must thank Peter Hodson for responding to my Perspective, because it gives an opportunity to sharpen the focus on some of the issues. I am sure, however, that, indeed, this will not be "the last word on the subject" — Michael Gilbertson, *Fish Habitat Management Branch, Department of Fisheries and Oceans, 200 Kent St., Ottawa, Ont. K1A 0E6.* (J8102b)

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BOOK REVIEWS/COMPTES RENDUS

Toxic Contaminants in the Great Lakes. Vol. 14. *Edited by J. O. Nriagu and M. S. Simmons. John Wiley & Sons, Inc. Somerset, NJ. 1984. 527 p. $95 U.S.*

The volume is the 14th in the Wiley Series on Advances in Environmental Science and Technology, and as with each of the other volumes in the series is a well-bound, nicely formatted, typeset volume, which is free of errors.

Until the publication of this volume there was no concise anthology of literature about contaminants in the Laurentian Great Lakes. A large body of literature had accumulated in a broad spectrum of journals and government reports, and the literature was replete with documentation of the contamination of all compartments of the Great Lakes ecosystem. However, there was no synthetic compendium of these results.

This volume contains 19 chapters contributed by recognized experts. Sixteen of the chapters deal mostly with organic contaminants. This is appropriate, since it has been concluded that significant impacts of inorganic contaminants are restricted to a few localized sediment contamination problems. In general the concentrations of trace inorganic contaminants are much smaller than concentrations which elicit adverse effects. The volume provides information on pesticides, polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAH), lead, selenium, and other trace materials.

The first chapter outlines the potential hazard of PCBs to humans from consumption of fish from the Great Lakes. The chapter is well written and reflects the literature, which has been primarily on PCBs but does not address other contaminants. While the title of this chapter is somewhat of a misnomer because it leads the reader to believe that more contaminants were considered, it was written in a very logical manner and elucidated the rational for establishment action levels for PCB concentrations in fish from the Great Lakes.

Because this volume is an anthology of contributed papers, it suffers from the unevenness of different writing styles and numerous redundancies. For instance, extensive backgrounds are given four times for PCBs and twice for toxaphene. While all of the contributors are recognized experts and the individual chapters well written, the format relegates the volume to reference text status. The essentials of many of the papers appear elsewhere as government reports or publications in journals or both.

The volume is successful as a state of the art compendium and will be a very useful reference volume. The chapters are complete, concise, and well referenced, with pertinent reference through early 1982. The writing style, for the most part, is extremely readable and the editors were successful in eliminating jargon and inserting explanations of technical terms. Therefore, everyone with an interest in trace contaminants in the Great Lakes will find this an understandable reference volume. The index is adequate but not extensive for secondary topics and is not extensively cross-indexed.

The authors seem to have been encouraged to provide a definitive statement on the state of the art, relative to each title. This was only partly successful. Several chapters do give "hard hitting" conclusions and suggest what future research is necessary.

The knowledge of transfer mechanisms of trace contaminants in the Great Lakes is reported in detail. While several chapters were written to deal with these subjects extensively, much of the interesting and worthwhile information is found throughout the volume. The information on nonpoint, aerial inputs and the surface microlayer is discussed in detail. The sedimentary record is discussed in one chapter but received much less attention.

Little information was presented on radioisotopes, which is unfortunate because there have been a number of very good studies conducted and much of this information is found in "grey-literature" of government reports and symposium proceedings, which is not readily available to most readers. It is this literature that because of the utility of isotopic tracers has provided much of the insight into sedimentation rates, resuspension, and basic dynamics of materials within the Great Lakes basins. The information embodied in that literature has often not been considered as we turn to the organic contaminants which have gained prominence in recent years.

This volume reflects the state of knowledge about toxic contaminants in the Great Lakes, in that most of the information is on monitoring contaminants and understanding the mechanisms of disposition within the environment. Dose is only one component of a hazard assessment. The other aspect is the dose–response relationship. Even when laboratory toxicity studies are available, it has been difficult to determine the laboratory to field applicability. At present our ability to answer questions about the effects of trace contaminants is severely limited.

Future research should be directed toward gathering the information to answer questions such as: What adverse effects do present concentrations of contaminants have? What concentrations will be needed to elicit a particular response in the future? What are the interactions among compounds under field conditions? In my opinion, we have been gathering the information which is easiest to obtain. While the monitoring and fate studies are not simple, to gain credibility with the public in general and decision makers in particular, it is now time to address the question of how hazardous the toxic contaminants in the Great Lakes are.

I bought a copy of this volume and feel that it is a must for limnologists, ecologists, and toxicologists working on the Great Lakes. This is one of the most comprehensive, readable volumes of its type that I have on my bookshelf.

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Methods in Marine Zooplankton Ecology. *M. Omori and T. Ikeda. Wiley-Interscience, New York, NY. 1984. 332 p. $44.95 U.S.*

Although the title suggests a methods cookbook, this is actually more of a graduate level teaching and reference text on marine zooplankton ecology. The book succeeds very well in this role. Individual chapters cover the classical topics and activities in zooplankton ecology: sampling, fixation and preservation, identification and enumeration, measurement of biomass and chemical composition, live animal maintenance, feeding rate, metabolic rate, estimation of growth, mortality, and secondary productivity, and description of species distributions and associations. The treatment of these topics is generally balanced and thorough. In most cases, the authors describe two or more methodological approaches to a given measurement problem, evaluate their relative strengths and weaknesses, and briefly summarize, with well-chosen examples from the literature, the current state of knowledge and interpretation. I found very few statements to quarrel with, and these disputes were of the nit-picking variety (e.g. their interpretation of the gut clearance curve shown on p. 160 as a starvation effect rather than a constant exponential turnover rate). A more significant criticism is that the range of topics and methods is traditional and rather conservative. For example, biochemical techniques, microzooplankton rate measurements, field and laboratory measurement of swimming activity, interaction with higher trophic levels, and response (both organism and community level) to environmental variability are underrepresented relative to current research activity. The historical perspective of the book enhances its unity and clarity as a text but somewhat reduces its value as a current and comprehensive methods manual.

Presentation of the material is technically excellent. Despite the potential for translation problems (the book is a revision and expansion of a 1976 Japanese language edition by the same authors), the language is clear and very readable. Typographic errors and/or translation glitches are present (perhaps 0.05–0.1 per page) but do not obscure the meaning of the text. The authors have also included a large number of figures and tables to illustrate both apparatus and results. The sketches of simple and low-cost "homemade" devices for sorting, stirring, washing, and rearing experimental organisms are especially valuable. The reference list is cosmopolitan and reflects the international reputation and research experience of the authors.

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(R632)

ANNOUNCEMENTS/AVIS

CCFFR–CCRP

Ottawa, 6–7 January 1986

Preliminary Program and Call for Papers

Two invited paper sessions are planned for 1986. The first, scheduled for Monday morning, is entitled "Habitat selection and its relation to fisheries" and will be convened by D. L. Kramer. The second, scheduled for Tuesday, is entitled "Quantitative genetics and its application to aquaculture and fisheries," and will be convened by J. D. McPhail. The Stevenson Lecture will be presented on January 6.

Contributed papers sessions are planned for both afternoons. ***This is a call for abstracts***. Type your abstract (maximum 200 words, single-spaced). Contributed papers will be selected by a committee of four; duration should be 15 minutes for discussion. Standard audiovisual equipment (35 mm and overhead projectors) will be available. We also plan to present posters; please indicate whether your paper should be considered as a poster or *could* be considered as a poster. Deadline for abstracts is August 30, 1985, and they should be sent to Dr. D. L. Kramer, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1.

CCFR–CCRP

Ottawa, les 6 et 7 janvier 1986

Programme préliminaire et demande de résumés

Deux séances avec des conférenciers invités sont au programme pour 1986. La première, prévue pour le lundi matin, s'intitule « La sélection de l'habitat et sa relation avec les pêches ». Elle sera animée par D. L. Kramer. La seconde, prévue pour mardi, s'intitule « La génétique quantitative et son application à l'aquiculture et aux pêches ». Elle sera animée par J. D. McPhail. La conférence à la mémoire de J. C. Stevenson aura lieu le 6 janvier.

Une séance de présentation de documents est prévue pour les deux après-midi. ***Nous vous invitons par la présente à envoyer vos résumés.*** Le résumé doit être dactylographié (200 mots au maximum, simple interligne). Les résumés présentés seront évalués par un comité de quatre personnes. Quinze minutes seront allouées à la discussion. Des appareils audio-visuels (projecteur 35 mm et rétroprojecteur) seront à votre disposition. Nous avons aussi l'intention de présenter des affiches; veuillez indiquer si votre résumé devrait ou *pourrait* être affiché. La date limite d'envoi des résumés a été fixée au 30 août 1985. Veuillez le faire parvenir à Dr D. L. Kramer, Département de biologie, Université McGill, 1205, avenue Docteur Penfield, Montréal (Qué.) H3A 1B1.

GAP: Third International Workshop

The Group for Aquatic Primary Productivity will hold its third international workshop at the National Institute for Water Research Regional Laboratory in Durban, South Africa, from April 27 to May 3, 1986. Its theme will be "Respiration and its effects on the measurement of aquatic primary productivity." This workshop will be a hands-on exercise where scientists from many disciplines will be working together calibrating and comparing their techniques for making measurements on seawater and water in clear and eutrophic impoundments.

The main objectives of the meeting will be the following:

(1) To assess the status of knowledge on aquatic primary production, with particular attention to current and future methodology.

(2) To perform joint field experiments using different techniques to test comparability and reliability, with emphasis on experimental work.

(3) To define gaps in knowledge and assess research goals for the future.

For further information, contact the Symposium Secretariat S.372 at the following address: Council for Scientific and Industrial Research, Box 395, Pretoria, 00001 South Africa. Telephone: National (012) 86-9211 X 2286 or 2879 (Jill Sawers), X 3580 (Richard Robarts). Telex: 3-21312 SA. Telegrams: NAVORSLIG.

GAP : Troisième atelier international

Le Group for Aquatic Primary Productivity tiendra son troisième atelier international au National Institute for Water Research Regional Laboratory à Durban (Afrique du sud) du 27 avril au 3 mai 1986. L'atelier aura pour thème « La respiration et ses effets sur la mesure de la productivité aquatique primaire ». Il s'agira d'un exercice pratique où des scientifiques de nombreuses disciplines travailleront ensemble à calibrer et à comparer leurs techniques de mesure relatives à l'eau de mer et à l'eau des étangs limpides et eutrophes.

Voici les principaux objectifs de la réunion :

(1) Évaluer l'état des connaissances sur la production primaire aquatique, en particulier les méthodes actuelles et futures.

(2) Réaliser conjointement des expériences sur le terrain à l'aide de différentes techniques pour en tester la comparabilité et la fiabilité, en insistant sur le travail expérimental.

(3) Définir les lacunes dans les connaissances et évaluer les objectifs de recherche pour l'avenir.

Pour plus de renseignements, communiquer avec le secrétariat de l'atelier S.372 à l'adresse suivante : Council for Scientific and Industrial Research, Box 395, Pretoria, 00001 South Africa. Téléphone : National (012) 86-9211 X 2286 or 2879 (Jill Sawers), X 3580 (Richard Robarts). Télex : 3-21312 SA. Télégrammes : NAVORSLIG.

115th Annual Meeting of the American Fisheries Society

The 115th annual meeting of the American Fisheries Society will be held in conjunction with the 75th annual meeting of the International Association of Fish and Wildlife Agencies in Sun Valley, Idaho, September 7–12, 1985. The meeting will offer contributed papers, posters, and special sessions on a broad range of topics of wide geographic and professional interest.

Special session topics will include the following: Application of Remote Sensing to Fisheries; Fish Habitat Relationships; Rehabilitation of Depressed Salmon and Steelhead Runs in the Columbia River Basin; User Group Conflicts: Economic Elements; User Group Conflicts: Social Impacts; Water Quality Concerns: Real or Perceived; Riparian Ecosystem Management; Competitive Fishing — Challenges and Potential Impacts; Computer Utilization in Hatcheries; Problems with Gas Supersaturation; Tribal Governments as Comanagers of Fisheries Resources; and Gear Evaluation in Difficult Habitats. Full-day workshops are planned on Stock Assessment and Fisheries Education. Several Contributed Paper Sessions will be held including Freshwater and Marine Fisheries Management, Fish Population Dynamics, Pollution and Toxicology, Physiology and Genetics, and Fish Ecology. Social activities and tours will make good use of Sun Valley's beautiful mountain setting.

All program-related questions should be directed to R. G. White, 1985 AFS Program Chairman, Montana Cooperative Fishery Research Unit, Biology Department, Montana State University, Bozeman, MT 59717, USA (telephone: 406-994-3491). Questions regarding meeting facilities and arrangements should be directed to Jim Keating, Arrangements Coordinator, 5203 Hill Road, Boise, ID 83703, USA (telephone: 208-342-4401).

115e réunion annuelle de l'American Fisheries Society

La 115e réunion annuelle de l'American Fisheries Society aura lieu en même temps que la 75e réunion annuelle de l'International Association of Fish and Wildlife Agencies à Sun Valley (Idaho) du 7 au 12 septembre 1985. La réunion offrira des séances de présentation de documents, d'affichage, et des séances spéciales sur une large gamme de sujets d'intérêt géographique et professionnel très vaste.

Les séances spéciales porteront entre autres sur l'application de la télédétection aux pêches; les relations de l'habitat du poisson; la remise en état de la faible remonte du saumon et de la truite arc-en-ciel dans le bassin du fleuve Columbia; les conflits entre les groupes d'utilisateurs : éléments économiques; les conflits entre les groupes d'utilisateurs : répercussions sociales; les préoccupations relatives à la qualité de l'eau : réelles ou perçues; la gestion de l'écosystème des rives; la concurrence en matière de pêche — défis et répercussions éventuelles; l'utilisation de l'ordinateur dans les piscifactures; les problèmes concernant la sursaturation gazeuse; les gouvernements des tribus : cogestionnaires des ressources halieutiques; et l'évaluation des engins dans les habitats difficiles. Des ateliers d'une journée sont prévus sur l'évaluation des stocks et l'information en matière de pêche. Plusieurs séances de présentation de documents seront organisées, notamment sur la gestion des pêches en mer et en deux douces, la dynamique des populations de poissons, la pollution et la toxicologie, la physiologie et la génétique et l'écologie des poissons. Pour les activités sociales et les excursions, on tirera parti du beau cadre montagneux de Sun Valley.

Toutes les questions relatives au programme devraient être adressées à R. G. White, 1985 AFS Program Chairman, Montana Cooperative Fishery Research Unit, Biology Department, Montana State University, Bozeman, MT 59717 (États-Unis) (téléphone : 406-994-3491). Les questions concernant les installations de la réunion et les autres arrangements devraient être adressées à Jim Keating, Arrangements Coordinator, 5203 Hill Road, Boise, ID 83703 (États-Unis) (téléphone : 208-342-4401).

1985 W. F. Thompson Award

American Institute of Fishery Research Biologists

In recent years the American Institute of Fishery Research Biologists (AIFRB) has presented an award to the student writing the best paper published during subsequent three-year periods. The award is the W. F. Thompson Award and the person receiving it would receive a certificate from AIFRB, as well as a check for $750.

The award committee of AIFRB is now receiving nominations for the 1985 W. F. Thompson Award which will cover the period 1982–1984. Papers can have multiple authors, but the student nominated for the award must be the principal author. Peers and professors can be listed as junior authors. Where a student receives the award and certificate for a multiple-authored paper, the professor will receive a certificate acknowledging his role in the outstanding paper.

Papers should be concerned with freshwater or marine fisheries topics and problems, and may deal with biology or

Prix W. F. Thompson 1985

American Institute of Fishery Research Biologists

Ces dernières années, l'American Institute of Fishery Research Biologists (AIFRB) a décerné un prix récompensant l'étudiant ayant rédigé le meilleur article publié au cours d'une période de trois ans. Il s'agit du prix W. F. Thompson dont le lauréat reçoit un certificat de l'AIFRB ainsi qu'un chèque de 750 $).

Le Comité du prix de l'AIFRB reçoit actuellement les nominations pour le prix W. F. Thompson 1985 qui couvrira la période de 1982 à 1984. Les articles peuvent avoir plusieurs auteurs, mais l'étudiant proposé pour le prix doit en être l'auteur principal. Les collègues et les professeurs peuvent être mentionnés comme collaborateurs. Lorsqu'un étudiant obtient un prix et un certificat pour un article à plusieurs auteurs, le professeur recevra un certificat reconnaissant sa collaboration à l'article primé.

Les articles doivent traiter des questions et des problèmes

management problems. The papers are evaluated by the AIFRB award committee on the basis of originality, organization and development, and pertinence to current problems in fisheries. Nominations for papers should be received ***no later than 15 July 1985***. A final decision will be announced by 31 August 1985. Seven copies of each paper nominated should be sent to Dr. W. (Tony) Kwain, Chairman, AIFRB W. F. Thompson Award Committee, Ontario Ministry of Natural Resources, Lake Superior Fisheries Research Unit, P.O. Box 130, Sault Ste. Marie, Ontario, Canada P6A 5L5.

If there are questions in regard to the award, the Chairman can be reached at (705) 949-1231, extension 274.

concernant la pêche en mer ou en eau douce; ils peuvent porter sur les problèmes de biologie ou de gestion. Les articles sont évalués par le Comité du prix de l'AIFRB en fonction de leur originalité, leur plan, leur contenu et leur pertinence par rapport aux problèmes courants de la pêche. Les articles proposés devront lui parvenir ***pour le 15 juillet 1985 au plus tard***. L'article choisi sera annoncé pour le 31 août 1985. Sept exemplaires de chaque article proposé doivent être envoyés au Dr W. (Tony) Kwain, président, Comité du prix W. F. Thompson de l'AIFRB, Ministère ontarien des Richesses naturelles, Lac Supérieur, Service de recherche sur les pêches, C.P. 130, Sault-Ste-Marie (Ontario), Canada P6A 5L5.

Pour toute question sur le prix, on peut communiquer avec le président au (705) 949-1231, poste 274.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Winter distribution of ringed seals (*Phoca hispida*) in the Barrow Strait area, Northwest Territories, determined by underwater vocalizations **W. Calvert and I. Stirling**

Use of a bacterial bioluminescence assay to assess toxicity of contaminated marine sediments **M. H. Schiewe, E. G. Hawk, D. I. Actor, and M. M. Krahn**

Excess unsupported ^{210}Pb in lake sediment from Rocky Mountain lakes: a groundwater effect **S. A. Norton, C. T. Hess, G. M. Blake, M. L. Morrison, and J. Baron**

An improved photo-electric fish egg counter **R. W. Tanasichuk, C. Armstrong, and D. M. Ware**

Aggregative response of common mergansers (*Mergus merganser*): predicting flock size and abundance on Vancouver Island salmon streams **C. C. Wood**

Influence of the insecticide Diflubenzuron (Dimilin) on the growth of marine diatoms and a harpacticoid copepod in culture **N. J. Antia, P. J. Harrison, D. S. Sullivan, and T. Bisalputra**

Evidence of contaminant loading to Lake Ontario from the Niagara River **A. H. El-Shaarawi, S. R. Esterby, N. D. Warry, and K. W. Kuntz**

Adjuvant-dependent immunity and the agglutinin response of fishes against *Aeromonas salmonicida*, cause of furunculosis **R. C. Cipriano and S. W. Pyle**

Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river **D. A. Soluk**

Nutrient dynamics in a littoral sediment colonized by the submersed macrophyte *Myriophyllum spicatum* **R. Carignan**

Notes

Ultrasound imaging used to detect cysts of *Henneguya salminicola* (Protozoa: Myxozoa) in the flesh of whole Pacific salmon **N. P. Boyce**

Standing stock and production of fish in a cascading lake system on the Canadian Shield **J. R. M. Kelso**

Adenovirus-like particles associated with a disease of cultured white sturgeon, *Acipenser transmontanus* **R. P. Hedrick, J. Speas, M. L. Kent, and T. McDowell**

Letters and comments/Lettres et commentaires

Correction in use of oxycalorific equivalent **J. R. Brett**

Book reviews/Comptes rendus

Engineering approaches for lake management, Volume 1: Data analysis and empirical modeling; Volume 2: Mechanistic modeling (Kenneth H. Reckhow and Stephen C. Chapra) **P. J. Dillon**

Books received/Livres reçus

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 42, No. 6, June 1985

Volume 42, nº 6, juin 1985

Articles

Are age-structured models appropriate for catch-effort data? D. Ludwig and C. J. Walters **1066–1072**

Yolk absorption, yolk sac constrictions, mortality, and growth during first feeding of Atlantic salmon (*Salmo salar*) incubated on astro-turf T. J. Hansen and D. Møller **1073–1078**

Factors affecting variability of trapnet catches J. M. Hamley and T. P. Howley **1079–1087**

Responses of *Isonychia bicolor* to alkaline pH: an evaluation of survival, oxygen consumption, and chloride cell ultrastructure G. T. Peters, D. S. Cherry, and J. Cairns, Jr. **1088–1095**

Relationship of crayfish (*Orconectes virilis*) growth to population abundance and system productivity in small oligotrophic lakes in the Experimental Lakes Area, northwestern Ontario R. L. France **1096–1102**

Chemistry of Lake Hovvatn, Norway, following liming and reacidification R. F. Wright **1103–1113**

Planktivory in a littoral-dwelling lake fish association: prey selection and seasonality A. Keast **1114–1126**

Effective solvents and extraction periods employed in phytoplankton carotenoid and chlorophyll determinations N. D. Bowles, H. W. Paerl, and J. Tucker **1127–1131**

The influence of fish–zooplankton–phytoplankton interactions on the results of selenium toxicity experiments within large enclosures A. Salki, M. Turner, K. Patalas, J. Rudd, and D. Findlay **1132–1143**

Biology of the bathylagid fish, *Leuroglossus schmidti*, in the Strait of Georgia, British Columbia, Canada J. C. Mason and A. C. Phillips **1144–1153**

Recent changes in the inshore forage fish of Lake Michigan D. J. Jude and F. J. Tesar **1154–1157**

Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed M. Fréchette and E. Bourget **1158–1165**

Food-limited growth of *Mytilis edulis* in relation to the benthic boundary layer M. Fréchette and E. Bourget **1166–1170**

Organic nitrogen compounds in atmospheric precipitation: their chemistry and availability to phytoplankton M. H. Timperley, R. J. Vigor-Brown, M. Kawashima, and M. Ishigami **1171–1177**

Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens* L. G. Rudstam and J. J. Magnuson **1178–1188**

The distribution and abundance of seals in the Canadian high Arctic, 1980–82 M. C. S. Kingsley, I. Stirling, and W. Calvert **1189–1210**

Fish production in warmwater streams in Poland and Ontario R. Mahon and E. K. Balon **1211–1215**

Notes

Phytoplankton response to freshwater runoff: the diversion of the Eastmain River, James Bay R. G. Ingram, L. Legendre, Y. Simard, and S. Lepage **1216–1221**

The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams C. J. Cederholm and N. P. Peterson **1222–1225**

Letters and comments/Lettres et commentaires

Comment P. V. Hodson **1226–1228**

Reply M. Gilbertson **1228–1230**

Book reviews/Comptes rendus

Toxic contaminants in the Great Lakes. Vol. 14 (edited by J. O. Nriagu and M. S. Simmons) J. P. Geisy **1231**

Methods in marine zooplankton ecology (M. Omori and T. Ikeda) D. L. Mackas **1232**

Announcements/Avis **1233–1235**

Coming next month/À paraître le mois prochain **1236**

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